

TWO UPPER CRETACEOUS SALMONIFORM FISHES FROM THE LEBANON

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CONTENTS

	<i>Page</i>
I. INTRODUCTION	208
II. MATERIAL AND METHODS	208
III. DESCRIPTION	209
(a) General	209
(b) Systematic	209
<i>Gaudryella</i> gen. nov.	210
<i>G. gaudryi</i> (Pictet & Humbert)	210
<i>Humbertia</i> gen. nov.	231
<i>H. aperta</i> sp. nov.	232
IV. DISCUSSION	250
(a) Similarities between <i>Gaudryella</i> and <i>Humbertia</i> and evidence of euteleostean relationships	250
(b) Differences between <i>Gaudryella</i> and <i>Humbertia</i> and relation- ships within the Euteleostei	252
(i) Ethmoid region	259
(ii) Jaws and dentition	265
(iii) Hyoid and branchiostegals	268
(iv) Caudal skeleton	269
(v) Conclusions	278
(c) Comparisons with <i>Clupavus</i> and the Clupavidae	283
(d) Comparisons with other Cretaceous teleosts	288
V. SUMMARY	290
VI. REFERENCES	291
VII. ABBREVIATIONS USED IN FIGURES	296

SYNOPSIS

Two small, unspecialised teleosts, *Gaudryella* gen. nov. *gaudryi* (Pictet & Humbert) and *Humbertia aperta* gen. & sp. nov., are described in detail on the basis of abundant acid-prepared material from the Middle Cenomanian fish beds of Hakel and Hajula, Lebanon. These fishes are superficially very similar, but differ in many anatomical features, some of considerable importance. Despite these differences, it is not possible to show that either species is more closely related to any living or Cretaceous fish than is the other. The only group with which they show positive evidence of relationship is the salmoniform subgroup containing the Osmeroidei and Stomiatoidei, especially the hypomesine osmerids, but these relationships are not sufficiently close to place either genus in one of these suborders, and they are left as Salmoniformes *incertae sedis*. The Upper Jurassic and Cretaceous family Clupavidae is reviewed and is found to contain poorly known, superficially similar species whose relationships are largely unknown. The ethmoid ossifications of teleosts and the caudal skeletons of euteleosts are discussed, and a hypothesis of euteleostean interrelationships is suggested on evidence from the caudal skeleton.

I. INTRODUCTION

THIS paper contains detailed accounts of two superficially similar, *Clupavus*-like teleosts, with a discussion of their relationships and of the status of the family Clupavidae. In 1967 I published "preliminary reconstructions" of the skull and caudal skeleton of "an as yet undescribed species of *Clupavus*" from the Cenomanian fish beds outcropping at Hakel and Hajula in the Lebanon (Patterson 1967b, figs. 9-11; see also Patterson 1967a : 72). These reconstructions were made in order to demonstrate that the genus *Clupavus* Arambourg and the family Clupavidae, as then understood, were not close relatives of the clupeomorph fishes, with which they had previously been placed. Recently I took up the material of this "*Clupavus* sp." again in order to prepare a detailed description. After making transfer preparations of more specimens and puzzling over the available material for several weeks, I eventually realized that it was not conspecific: two species are present, superficially very similar, of which one is abundant and the other relatively rare, and while my preliminary restorations of the skull were based almost entirely on the commoner form, the restoration of the caudal skeleton was a composite of the two. Once I had learned to distinguish these two species, and had obtained more specimens of the rarer species from the large collection of fishes from Hajula in the American Museum of Natural History, New York, I found that the differences between the two are rather profound. They are described below as different genera, but their relationship is almost certainly more distant. The problem of assessing the significance of the similarities and differences between these two Cretaceous species, both in regard to their interrelationships and their relationships with contemporary and living teleosts, raises various questions concerning the evolution and structure of the Euteleostei, which are discussed below. This is the second of a series of papers based primarily on material collected by the author in the Lebanon in 1964.

I am indebted to Dr. Bobb Schaeffer, American Museum of Natural History, and to Prof. Camille Arambourg and Mlle Jean Signeux, Museum d'Histoire Naturelle, Paris, for the loan of specimens, and to Sci. mag. Niels Bonde, Copenhagen, for information about various clupavid specimens in European museums. I am most grateful to Dr. P. H. Greenwood and Dr. D. E. Rosen for valuable discussions and advice, to Dr. S. H. Weitzman for reading and commenting on the manuscript, and to Mr. C. I. Macadie for introducing me to the value of radiographs of transfer preparations. The photographs were taken by Mr. T. W. Parmenter.

II. MATERIAL AND METHODS

The fossil material described here is in the collections of the British Museum (Natural History), designated by register numbers with the prefix 'P.' or without prefix, and the American Museum of Natural History, referred to by the prefix 'AM'.

The descriptions are based almost entirely on acid prepared specimens, since the two genera are often extremely difficult to distinguish in unprepared material. Specimens were prepared by the transfer technique (Toombs & Rixon 1959)—etching away the matrix after embedding the fossil in epoxy resin—and a few skulls were prepared as free-standing objects by solution of the matrix from specimens in which the head was still unexposed. After study of enough of these preparations to

gain familiarity with the various bones of the two species, a good deal of valuable material was obtained by acid treatment of random blocks of rock from Hajula and sorting of the isolated bones in the residues. This method was particularly useful with *Gaudryella gaudryi*, since this is the most abundant fish at Hajula.

Radiographs of transfer preparations are sometimes very valuable, revealing features not visible by direct examination (cf. Pls 1, 3-5), and radiography is worth considering as a standard technique with all such preparations. Crude but useful histological study of transfer preparations can be carried out very simply, by partially filling the cavity in the resin block with xylene and examining the fish in transmitted light on the microscope stage.

III. DESCRIPTION

(a) General

The species described below as *Gaudryella* gen. nov. *gaudryi* (Pictet & Humbert) and *Humbertia operta* gen. & sp. nov. are usually to be found in museum collections undetermined or under the names *Scombroclupea gaudryi* and *Scombroclupea* sp. (*Scombroclupea* is a clupeomorph genus, containing fishes easily distinguished from and unrelated to those described here). *Gaudryella gaudryi* and *Humbertia operta* occur at both Hakel and Hajula. Pictet & Humbert (1866) based their species *Clupea gaudryi* on six specimens from Hakel. At Hakel neither species is abundant, but they are probably commoner than their representation in museum collections would lead one to believe since these small, unremarkable looking fishes have not attracted collectors. At Hajula, *Gaudryella gaudryi* is very abundant and is certainly the commonest fish, a position filled at Hakel by the clupeomorph *Diplomystus brevissimus*, which is rare or absent at Hajula. *Humbertia operta* is much less abundant than *G. gaudryi* but is still quite common. The large collection of fishes from Hajula in the American Museum of Natural History (Hay 1903) seems to have been made more or less at random, without selection according to the size, distinctiveness or rarity of the fossils. A sample of 72 '*Scombroclupea* sp.' from this collection contained 17 *Humbertia operta* and 55 *Gaudryella gaudryi*, a ratio of about 25% : 75%, which is probably a fairly good estimate of their relative abundance. From Hakel, a much smaller sample is available, but the BM(NH) has six *Gaudryella gaudryi* and two *Humbertia operta*, indicating, probably by chance, exactly the same proportions.

There is no apparent ecological difference between *Gaudryella* and *Humbertia*, since at Hajula specimens of the two sometimes occur side by side on the same bedding plane. *Gaudryella gaudryi* was possibly a shoaling fish, since several individuals often occur on one bedding plane. *Humbertia operta* was more probably solitary, since no such multiple occurrences are known.

(b) Systematic

Division TELEOSTEI (*sensu* Nelson 1969a)

Cohort EUTELEOSTEI (Greenwood *et al.*, 1967)

Superorder PROTACANTHOPTERYGII (Greenwood *et al.*, 1966)

Order SALMONIFORMES

Suborder and family *incertae sedis*

Gaudryella gen. nov.

DIAGNOSIS. Small, slender, round-bodied salmoniform fishes ; parietals in contact medially and bearing the supratemporal commissure, post-temporal fossa roofed ; nasals short and trough-like ; rostral and mesethmoid separate, rostral much as in *Megalops* but without ethmoid commissure, mesethmoid ossified endo- and perichondrally ; vomer toothed and with long posterior process, parasphenoid toothless and without basiptyergoid process ; occipital condyle formed by basioccipital only, intercalar small, otolith chamber not inflated, orbitosphenoid and basisphenoid present, sclerotic ossified ; large supraorbital, antorbital, lachrymal, three infraorbitals and large dermosphenotic present, posterior infraorbitals extending to preopercular, uppermost infraorbital probably representing two fused bones ; hyomandibular vertical, double-headed, quadrate condyle below centre of orbit, metapterygoid reduced, no palatine or pterygoid teeth ; gape small, premaxilla small, simple and toothless, maxilla toothed, curved, not extending to middle of orbit, two mobile supramaxillae ; mandible with long, high coronoid process, dentary with short, steeply ascending oral border, few small teeth, a moderately large pocket on its inner face and the symphysis serrated ; distal ceratohyal perforate, basihyal unossified but heart-shaped basihyal tooth plate present ; 11 branchiostegals, the last two spathiform ; long, toothless gill-rakers on gill arches ; no suprapreopercular, subopercular not enlarged ; about 43 vertebrae, 15 caudal, anterior neural arches autogenous, about 7 supraneurals above anterior vertebrae, simple epineurals and epipleurals on abdominal vertebrae, anterior epineurals fused with neural arches ; mesocoracoid, two postcleithra and several distal pectoral radials present ; pelvics inserted below hind end of dorsal fin and with 12-13 rays, pelvic splint fused with girdle ; dorsal fin short, at mid-point of back, anal small and remote ; PU₂ with short, leaf-like neural spine, small lamellar expansions on neural spine of PU₃ and haemal spines of PU₂₋₃ ; PU₁, U₁, stegural, parhypural and lower hypurals fused, U₂ separate ; third and fourth hypurals fused, fifth and sixth autogenous ; stegural forked proximally, second uroneural present ; two epurals ; caudal fin forked, 19-rayed, one urodermal and reduced caudal scutes present ; scales large, very thin, cycloid, not extending on to skull or fins, lateral line complete ; skeleton mainly acellular.

TYPE (and only) SPECIES. *Clupea gaudryi* Pictet & Humbert (1866).

Gaudryella gaudryi (Pictet and Humbert)

Pl. 1, figs. 1, 2 ; Pl. 2, fig. 1 ; Pl. 3, fig. 2 ; Pl. 4, fig. 1 ; Pl. 5, fig. 1 ; Figs. 1-14, 30-33.

1866 *Clupea gaudryi* Pictet & Humbert : 60, pl. 5, figs. 2-5.

? 1879 *Clupea gaudryi* Pictet & Humbert ; Bassani : 163.

? 1882 *Clupea-gaudryi* Pictet & Humbert ; Bassani : pl. 7, figs. 1-4.

1901 *Scombroclupea gaudryi* (Pictet & Humbert) Smith Woodward : 138, *partim* (specimen 49503 only).

1967a *Clupea gaudryi* Pictet & Humbert ; Patterson : 72.

1967b *Clupavus* sp. Patterson, figs. 9, 10 (*non* fig. 11).

DIAGNOSIS. *Gaudryella* reaching about 90 mm. in standard length ; mean pro-

portions (as % standard length) : total length 116, head length 28, trunk depth 18, predorsal length 44·5, predorsal length 84·5, prepelvic length 58·5 ; 41–44 vertebrae, mean 43 ; D ii, 10 ; A ii, 7 ; P 15–16 ; V 12–13 ; C v–vii, I, 9, 8, I, vii–ix ; 6–8 scales in a transverse series on the trunk, about 45 lateral line scales.

LECTOTYPE. Pictet & Humbert figured three specimens of this species which are in the Musée d'Histoire naturelle, Geneva. The specimen illustrated in pl. 5, fig. 4 is selected as lectotype.

HORIZON AND LOCALITIES. Middle Cenomanian, Hakel and Hajula, Lebanon. Possibly also occurring in the Lower Cenomanian of Lesina, Dalmatia (Bassani 1882 ; see p. 288).

MATERIAL. Six specimens from Hakel in the BM(NH) and numerous specimens from Hajula in the BM(NH) and the American Museum of Natural History, especially the following acid prepared specimens : 49503, P.13875, P.13876, P.48224 (all Hakel), P.9991 (Pl. 2, fig. 1, Figs. 9, 10, 12C, 13A), P.48045, P.48047 (Pl. 1, figs. 1, 2, Fig. 6), P.48048/9, P.48050/1 (Fig. 5), P.48063, P.48065, P.51242, P.51243, P.51244 (Fig. 1), AM 3783 (four individuals together with two disarticulated *Humbertia aperta*, Pl. 4, fig. 1), AM 4115 (Pl. 5, fig. 1), AM 4599, AM 5568, AM 5579 (Fig. 14A) (all Hajula) ; and the following isolated bones or parts of the skeleton from Hajula : P.51245–6 (Fig. 2), P.51247–9 (Fig. 3) P.51250 (Fig. 4), P. 51251–3 (Fig. 7), P.51254 (Fig. 8), P.51255–6 (Fig. 11), P.51257 (Fig. 12A,B), P.51258 (Fig. 13B).

REMARKS. As previously noted (Patterson 1967a : 72), the specimens referred to *Scombroclupea gaudryi* by Smith Woodward (1901 : 138) are (except 49503) true *Scombroclupea*, probably *S. macrophthalma*, and are not conspecific with the type material of *Clupea gaudryi*, which lacks the abdominal scutes and anal finlets typical of *Scombroclupea*. D'Erasmus has referred to *Clupea gaudryi* (1922 : 72) and *Scombroclupea gaudryi* (1946 : 70) specimens from the Lower Cenomanian of Comen, near Trieste, which have abdominal scutes, forked intermusculars and anal finlets and are therefore also true *Scombroclupea*. Other specimens referred to this species by Bassani (1879, 1882) and Kramberger (1895) are discussed on p. 288.

DESCRIPTION. (i) *General features*. *G. gaudryi* is a small, slender, round-bodied fish. The largest individuals are about 90 mm. in standard length, but such large specimens are uncommon and the modal standard length is 60–70 mm. The body can have been only slightly laterally compressed since few specimens are preserved in lateral view, the usual mode of preservation of laterally compressed fishes. The dimensions of eight specimens are given in Table 1 : the variability of the proportional measurements is in part due to inaccuracies caused by twisting of the fishes during fossilisation, but the mean of these proportions seems to be fairly accurate.

(ii) *Skull roof and braincase*. The skull roof is partially shown in Figs. 1, 5 and 6, and is restored in Fig. 30. The skull roof is smooth and flat except for the raised tubes containing the sensory canals, and is long, with the anterior part of the frontals and the ethmoid drawn out into a slender snout. The supraoccipital (Soc) is small, with a short, thumb-like crest projecting posteriorly. The epiotics (Epo) border the supraoccipital and bear prominent articular surfaces for the post-temporals. The

parietals (Pa) meet in the mid-line, covering the anterior part of the supraoccipital, and join the epiotics in slightly digitate sutures. Laterally the parietals meet the pterotics (described on p. 216) forming the roof of the post-temporal fossa. There is a shallow transverse groove across the parietal, normally interrupted at a point which seems to be the centre of ossification of the bone. The lateral part of this groove is in line with the medial limb of the supratemporal and must have carried the supra-temporal commissure. The medial part of the groove, usually separated from the lateral part and often 'L'-shaped (Fig. 1), may represent the middle pit-line, but it is not possible to be certain of this.

TABLE I

Proportional measurements of eight specimens of *Gaudryella gaudryi*
as % standard length

Specimen	Standard length, mm.	Total length	Head length	Trunk depth	Predorsal length	Preanal length	Prepelvic length
P.13875 (Hakel)	45	—	30	18	42	84	58
P.13873 (Hajula)	51	118	29	18	45	82	55
P.13876 (Hakel)	54	—	29	20	44	84	56
P.48047 (Hajula)	67	—	28	15	48	87	63
P.46578 (Hakel)	71	—	24	20	42	82	54
P.48045 (Hajula)	72	—	26	18	40	86	56
P.13871 (Hajula)	73	116	30	18	48	85	66
AM 4146 (Hajula)	88	115	26	19	47	86	60
Mean	—	116	28	18	44.5	84.5	58.5

The frontals (Fr ; Fig. 3A) overlap the parietals posteriorly and the autosphenotics postero-laterally. Anteriorly the frontal tapers and ends as a thickened splint with a lamina of thin bone extending medially. The postero-lateral wing of the rostral lies on the upper surface of this lamina, fitting into the angle between it and the lateral, splint-like part (Fig. 1). The supraorbital sensory canal ran within the frontal in tubes which are slightly raised above the surface of the bone. At the postero-lateral corner of the frontal the canal passed out through a large pore and may have anastomosed with the temporal canal on the pterotic. There is a long, slender parietal branch of the canal passing back in a tube which opens at (Fig. 3A) or near (Fig. 1) the posterior margin of the frontal. A short postero-medial branch of the canal opens through a small pore at or just in front of the origin of the parietal branch. The epiphyseal branch passed medially in a tube which opens by a wide pore near the mid-line. There is one pore over the main canal anterior to the

epiphyseal branch. Anteriorly the canal left the frontal above the front of the orbit and passed to the nasal (Na, Figs. 1, 6), a small, trough-like bone.

The long, slender ethmoid region is occupied by the endochondral and perichondral mesethmoid and lateral ethmoids, and the dermal rostral (the homologies of the mesethmoid and rostral are discussed on p. 264). The rostral (Ro ; Figs. 1, 2, 5) is a

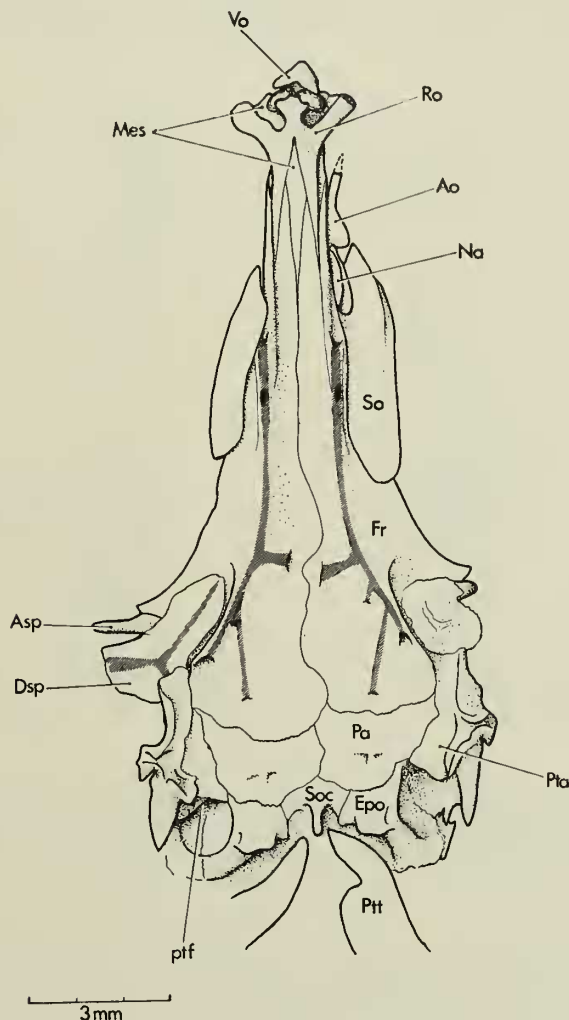


FIG. 1. *Gaudryella gaudryi* (Pictet & Humbert). Skull roof as preserved in P.51244, Hajula, Lebanon. Explanation of abbreviations p. 296.

superficial bone, not fused with the underlying mesethmoid. Anteriorly the bone has a median process and paired ventro-lateral wings, underlain by processes of the mesethmoid. Posteriorly there is a pair of very long, tapering processes which fit in

grooves on the upper surface of the frontal. There is no trace of a rostral commissure or pit-line. The mesethmoid (Mes ; Figs. 2, 5) is an extensive endochondral and perichondral ossification, fitting closely against the underside of the rostral. The perichondral upper surface of the bone (supraethmoid in Weitzman's (1967b) terminology) is exposed between the frontals and the posterior processes of the rostral (Fig. 1). Underneath the median anterior process of the rostral the mesethmoid has a similar but broader anterior process bearing a pair of large facets with which the

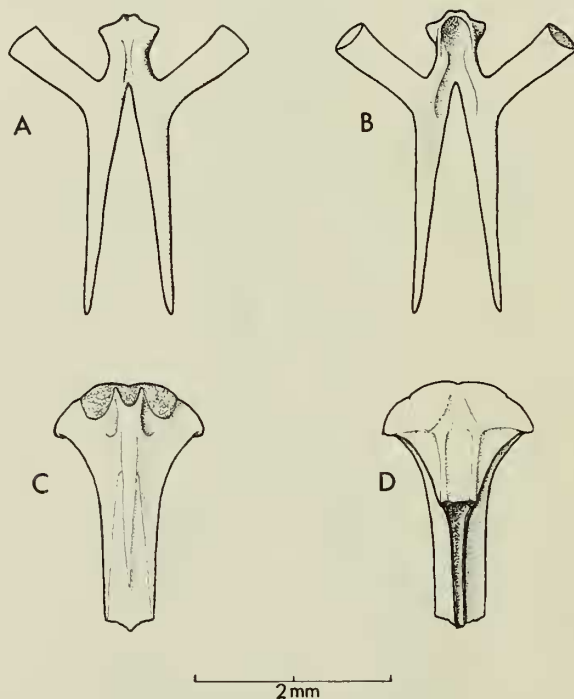


FIG. 2. *Gaudryella gaudryi* (Pictet & Humbert). Isolated rostral (A,B) and mesethmoid (C,D) in dorsal (A,C) and ventral view (B,D). Restorations based on P.51245 (rostral) and P.51246 (mesethmoid), Hajula, Lebanon. The mesethmoid is from a smaller individual than the rostral.

maxillae articulate. Below the ventro-lateral processes of the rostral there are processes of the mesethmoid ending in facets which articulate with the palatine. Posteriorly the mesethmoid extends back as a pair of vertical perichondral laminae which form the medial wall of the nasal capsules (capsular ethmoid bones in Weitzman's terminology). The lateral ethmoids are flimsy perichondral ossifications, usually covered by the large supraorbital.

The vomer (Vo, Figs. 1, 5, 9) is closely applied to the underside of the mesethmoid. Anteriorly the vomer ends in a projecting keel bearing a pair of large articular surfaces for the heads of the maxillae. Posteriorly the vomer has a very long shaft extending

back below the parasphenoid to the level of the centre of the orbit (Figs. 4, 9). Ten to twenty small teeth are borne in a single or partially double row on a median crest on the underside of the vomer. The parasphenoid (Pas ; Fig. 4) is slender and un-toothed. At the back of the orbit the parasphenoid broadens and has a large marginal notch for the efferent pseudobranchial artery (epsa), but there is no basipterygoid process. Posteriorly the parasphenoid ends in two wings below the basioccipital, with the posterior opening of the myodome between them.

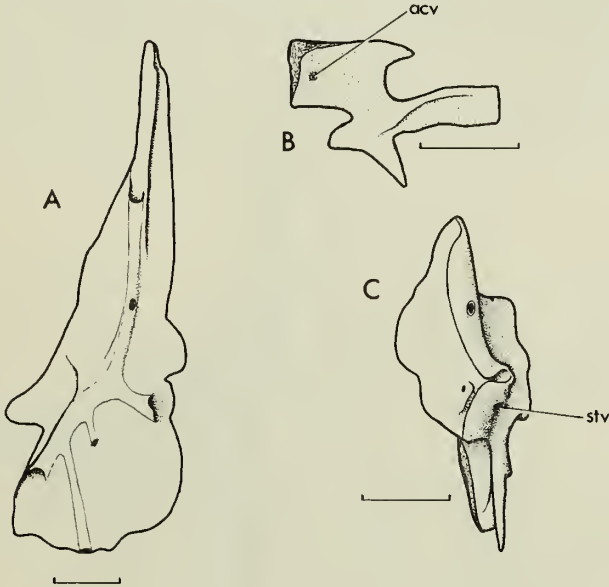


FIG. 3. *Gaudryella gaudryi* (Pictet & Humbert). Isolated left frontal (A, P.51247), orbitosphenoid (B, P.51248) and right pterotic (C, P.51249), from different individuals, Hajula, Lebanon. A, C, dorsal view, B, right lateral. Scale 1 mm. Explanation of abbreviations p. 296.

The endocranium (Fig. 4) is partially visible in several transfer preparations, but is best seen in P.51250, an isolated, crushed braincase, and in AMNH 3783. The endocranium shows no very remarkable features and will be described briefly. The occipital condyle is formed by the basioccipital alone. As noted above, the myodome (myo) opens posteriorly below the occipital condyle. The lateral wall of the saccular chamber is not inflated and there is no fenestra at the junction of the basioccipital (Boc), exoccipital (Exo) and prootic (Pro). The intercalar (Ic) is a small, superficial bone plastered over the junction of the exoccipital and pterotic on the postero-ventral angle of the braincase. There is no distinguishable subtemporal fossa, and no forward extension of the intercalar in this region. There is no indication of any association between the swimbladder and the ear, and there are no bullae in the prootic, pterotic or exoccipital. The trigemino-facialis chamber has at least three external openings, with those of the hyomandibular trunk (VII hm) and jugular vein (ptfc) separated by a short jugular canal. The oculomotor nerve passed through a

jecting from the lateral and posterior margins of the bone : although this covering flange effectively converts the sensory canal groove into a tube, it is open medially throughout its length. Posteriorly the sensory canal passed to the supratemporal, postero-laterally the preopercular canal left through a large groove, and anteriorly the canal passed to the dermosphenotic. If there was an anastomosis between the temporal and supraorbital canals it can only have lain superficial to the antero-medial part of the pterotic : there is no evidence of such an anastomosis on the bones and quite possibly it was not present. There is a small pore in the flange covering the anteriorly directed part of the sensory canal in the pterotic. Immediately behind the posterior, transverse part of the canal there is a large foramen (stv) leading dorso-laterally from the post-temporal fossa which probably transmitted the supratemporal branch of the vagus nerve. Behind this foramen the pterotic bears a long, membranous splint which extended back into the body musculature.

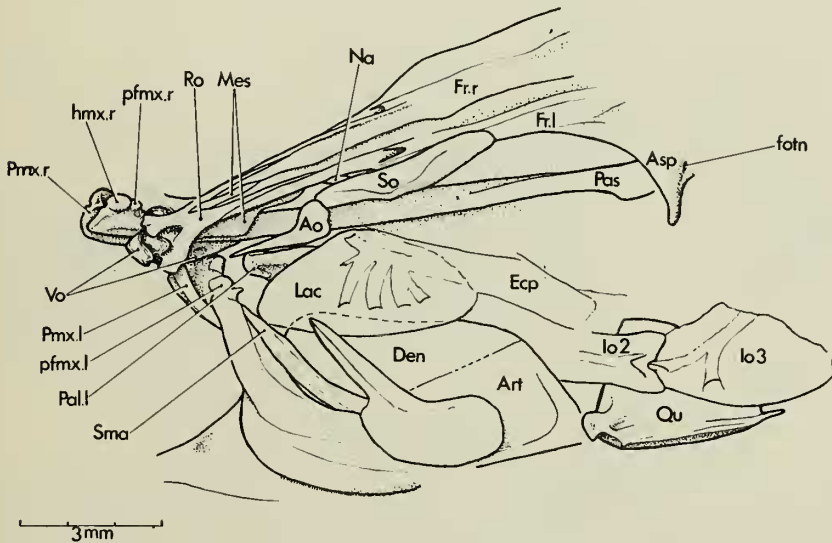


FIG. 5. *Gaudryella gaudryi* (Pictet & Humbert). Anterior part of skull as preserved in P.48051, Hajula, Lebanon. The suffixes 'r' and 'l' denote bones of the right and left side, explanation of other abbreviations p. 296.

The pterosphenoids (Pts) do not meet the mid-line and each has a notch in its ventral margin, probably marking the passage of the trochlear nerve (IV). There is a large, median orbitosphenoid (Ors ; Fig. 3B) with an anterior process passing forwards towards the lateral ethmoids below the olfactory nerves, and a stout ventral process extending downwards in front of the optic fenestra. There is a small foramen for the anterior cerebral vein (acv) in the posterior part of the orbitosphenoid. The sclerotic is ossified (scr, Fig. 6), probably in four pieces.

(iii) *Circumorbital bones.* The orbit is surrounded by seven bones, the dermosphenotic, three infraorbitals, the lachrymal, the antorbital and the supraorbital. There is

no evidence that the antorbital and supraorbital had any relation with the infra-orbital sensory canal.

The supraorbital (So, Figs. 1, 5, 6) is a large, oval bone, overlying the supraorbital flange of the frontal posteriorly and extending antero-ventrally. The anterior half of the bone has a ridge along its centre and is angular in section. The antorbital (Ao, Figs. 1, 5) is a small, comma-shaped bone, with a broad posterior part articulating with the lateral face of the supraorbital, and a slender anterior shaft fitting against the upper edge of the lachrymal.

The lachrymal and infraorbitals are very thin, flimsy bones. The lachrymal (Lac, Figs. 5, 6) is large and roughly triangular, meeting the antorbital above and overlapping the supramaxillae below. The infraorbital sensory canal passed through a tube near the upper edge of the bone, giving off three large branches which open near the ventral edge. The second infraorbital (Io2, Fig. 6) is a slender bone, about

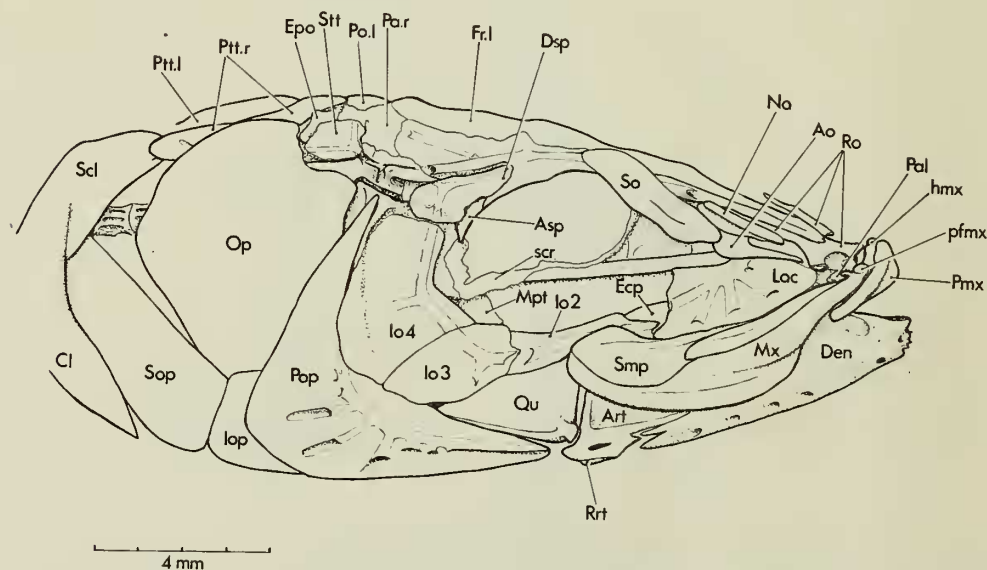


FIG. 6. *Gaudryella gaudryi* (Pictet & Humbert). Skull as preserved in P.48047, Hajula, Lebanon. The suffixes 'r' and 'l' denote bones of the right and left side, explanation of other abbreviations p. 296.

equal to the lachrymal in length, with the sensory canal passing through a tube along its centre. There is no evidence of pores or branches of the canal in the second infraorbital, but this is possibly due to deficiencies of preservation. The third infraorbital (Io3, Figs. 5, 6) is short but expanded posteriorly, extending back to the preopercular. The tube for the sensory canal runs some distance from the orbital margin of the bone, and is bent in the middle of the bone, giving off a short branch at this angle. Like the third, the large fourth infraorbital (Io4, Figs. 6, 9) is expanded, reaching the preopercular, and has the tube for the sensory canal some distance from

its orbital margin, with a bend midway down the bone and a branch passing back from this angle. Comparison with *Humbertia* (p. 239) and other primitive teleosts (see illustrations in Nelson 1969b) indicates that the large fourth infraorbital of *Gaudryella* incorporates the fourth and fifth infraorbitals. The presence of a branch and pore midway down the bone is positive evidence that such a fusion has taken place, because pores develop only between neuromasts, showing that the bone must contain two neuromasts, whereas there is only one in each posterior infraorbital of primitive teleosts.

The dermosphenotic (Dsp, Figs. 1, 6) is an elongate, triangular bone overlying the autosphenotic and frontal, covering the dilatator fossa. The dermosphenotic ends well short of the supraorbital, leaving a gap in the circumorbital series. The infraorbital canal ends blindly in the anterior part of the dermosphenotic, a short branch in the centre of the bone leading back to the temporal canal in the pterotic.

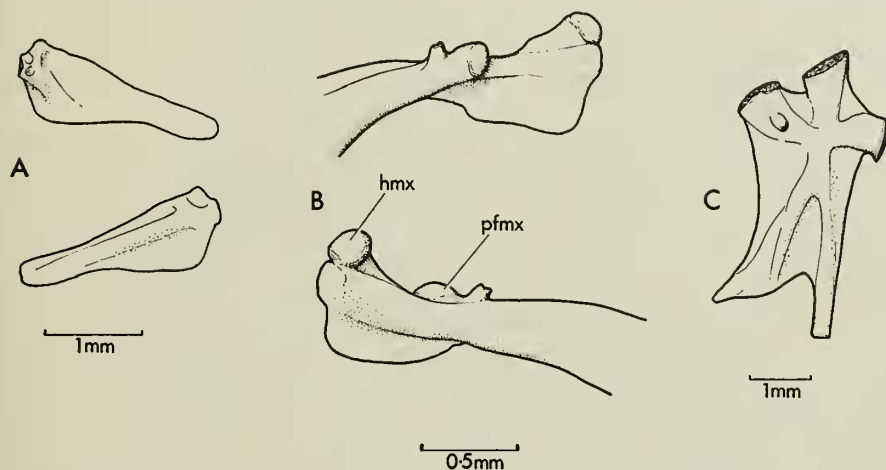


FIG. 7. *Gaudryella gaudryi* (Pictet & Humbert). A, isolated right premaxilla, P.51251, in internal (above) and external view. B, head of isolated right maxilla, P.51252, in external (above) and internal view. C, isolated right hyomandibular, P.51253, in medial view. All from Hajula, Lebanon. Explanation of abbreviations p. 296.

(iv) *Hyopalatine bones*. The hyomandibular (Hm ; Fig. 7C) is vertical or inclined slightly backwards. The head of the bone is divided into two portions, approximately equal in size. The opercular process lies in the upper third of the bone, opposite the foramen for the hyomandibular nerve on the medial surface of the bone. Ventrally the hyomandibular has a broad, membranous process extending antero-ventrally across the metapterygoid.

The metapterygoid (Mpt, Figs. 6, 9) is never clearly visible and seems to have been reduced. It consists of the usual two parts, an outer, 'D'-shaped lamina meeting the quadrate ventrally and covering the outer surface of the shaft of the hyomandibular, and a lamina extending dorso-medially to cover the posterior part of the endopterygoid and meet the antero-ventral process of the hyomandibular.

The symplectic (Sym, Fig. 9) is long and the quadrate (Qu, Figs. 5, 6, 9) is strongly inclined forwards, so that its postero-ventral margin is almost horizontal. The quadrate condyle lies below the centre of the orbit. The ectopterygoid (Ecp, Figs. 5, 9) is a slender, elongate bone, fitting against the anterior edge of the quadrate and curving forwards to meet the palatine. There is no sign of teeth on the ectopterygoid. The endopterygoid is a long, toothless lamina, supported by the palatine, ectopterygoid and metapterygoid, and articulating with the parasphenoid medially. The palatine (Pal, Figs. 5, 9) is straight, rather long, and toothless but heavily ossified. Anteriorly it ends in a large articular head, bearing a medially directed facet which articulates with the vomer and mesethmoid and a larger, laterally directed facet which articulates with a condyle on the upper edge of the maxilla.

(v) *Dermal upper jaw.* The dermal upper jaw consists of the premaxilla, maxilla and two supramaxillae. The premaxilla (Pmx, Figs. 5, 6 ; Fig. 7A) is a curved, toothless slip of bone, about one-quarter as long as the maxilla. An oblique ridge crosses the outer surface of the bone, ending in a rudimentary ascending process which fits against the condylar head of the maxilla, and there is a small internal process on the medial edge of the bone which was probably the site of insertion of the interpremaxillary ligament. There is no articular process.

The maxilla (Mx, Figs. 5, 6, 9) is deep and curved, ending in front of the level of the centre of the orbit. The head of the bone (Fig. 7B) is deep, with the cranial condyle (hmx) placed dorsally and a vertical flange below it which probably met its fellow in the mid-line. The cranial condyle articulated with the mesethmoid, the flange below it with the vomer. The ventral flange extends laterally behind the premaxilla. Lateral to the cranial condyle there is a large, rounded condyle (pfmx) on the dorsal surface of the maxilla which articulated with the head of the palatine (cf. Kirchhoff 1958, fig. 12 ; Gosline, Marshall & Mead 1966 ; Vrba 1968, fig. 3). Immediately behind this palatine condyle there is a postero-dorsally directed process on the maxilla which may have served for the insertion of the palato-maxillary ligament (cf. *Elops*, Vrba 1968 ; *Vinciguerria*, Weitzman 1967b ; and *Clupea*, Kirchhoff 1958), but whose shape is such that it must also have housed the ligament passing back to the lower jaw (cf. Gosline 1969 : 194 ; Weitzman 1967b : 516 ; Vrba 1968, *l. maxillo-mandibulare posterius*). Behind the premaxilla, the maxilla becomes deeper and blade-like. The oral border of this part of the bone is set with minute clustered teeth which extend on to the inner surface of the bone a little. The dorsal edge of the toothed part of the maxilla is shaped to accommodate the supramaxillae.

The anterior supramaxilla (Sma, Figs. 5, 6, 9) is a long, slender strap-like bone, ending just behind the process for the palato-maxillary ligament on the maxilla. The posterior supramaxilla (Smp, Figs. 5, 6, 9) has an ovoid body with a long anterior process extending above the posterior two-thirds of the anterior supramaxilla. The supramaxillae are displaced in specimens fossilised with the mouth open (Figs. 5, 9), showing that they were mobile, as in clupeoids (Kirchhoff 1958, fig. 39).

(vi) *Lower jaw.* The mandible (Fig. 8) is deep, with a short oral border and a high, rounded coronoid process. It consists of four bones, dentary, angulo-articular, retroarticular and a small ossification of Meckel's cartilage (sesamoid articular). The dentary (Den, Figs. 6, 8, 9) forms more than four-fifths of the upper and lower

borders of the jaw. The symphysis is moderately deep and has three or four characteristic antero-ventral projections or serrations, presumably for the insertion of symphyseal ligaments. Close to the symphysis there is a single row of five or six small, recurved teeth. Behind the teeth, the oral border of the dentary rises sharply into the coronoid process, as in *Leptolepis*, many clupeoids, *Coregonus*, *Hypomesus*, etc. The coronoid process has a concave anterior edge, and is highest anteriorly. At the base of the coronoid process, just behind the tooth row, there is a well marked depression on the outer face of the dentary for the insertion of the 'lip' ligaments (anterior maxillo-mandibular ligament). On the medial face of the dentary there is a moderately large pocket in which the angulo-articular is inserted.

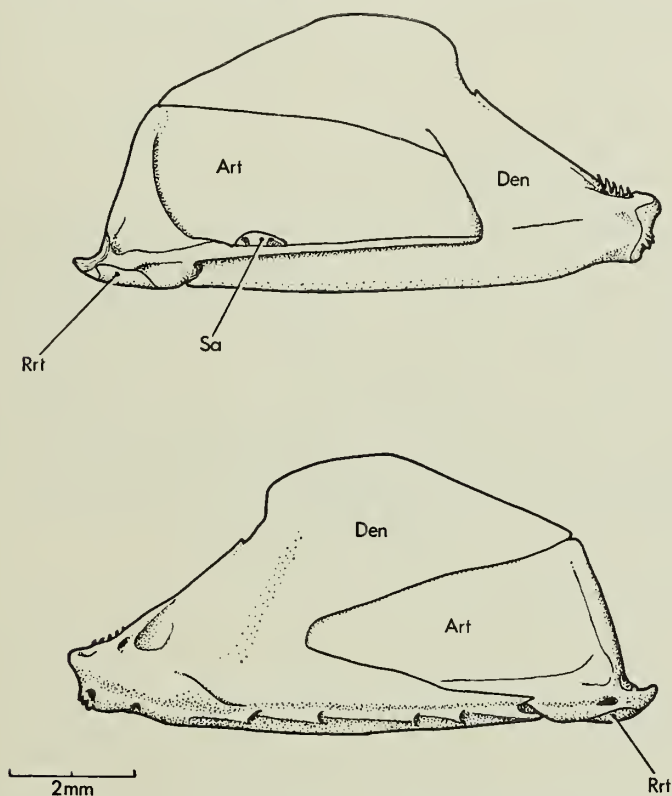


FIG. 8. *Gaudryella gaudryi* (Pictet & Humbert). Isolated left lower jaw in medial (above) and lateral view. P.51254, Hajula, Lebanon. Sa, sesamoid articular ; explanation of other abbreviations p. 296.

The dermal and endochondral portions of the angulo-articular (Art, Figs. 6, 8, 9) are indistinguishably fused. The articular surface for the quadrate is not deeply excavated, and there is only a very short retroarticular process. The coronoid process of the angulo-articular rises sharply in front of the articular facet, and the bone

extends forwards as a tapering lamina, fitting into the pocket in the dentary anteriorly. The mandibular sensory canal, passing forwards from the preopercular, entered the retroarticular process of the angulo-articular, passed through the bone with one elongate pore en route, and then traversed the dentary. There is a pore at the suture between the dentary and angulo-articular, and in the dentary there are four postero-ventrally directed branches opening by pores near the ventral edge of the bone, one pore below the anterior edge of the coronoid process, and one pore just behind the projections at the symphysis.

The retroarticular (Rrt, Figs. 6, 8, 9) is a small slip of bone applied to the postero-ventral surface of the angulo-articular. The sesamoid articular (Sa, Fig. 8) is a small half-cylinder of perichondral bone on the medial face of the angulo-articular.

(vii) *Hyoid arch and branchiostegals.* The hyomandibular is described above, with the palate. The interhyal is the usual short, waisted rod. The ceratohyal (Figs. 9, 32) is ossified in two pieces. The proximal ceratohyal (Pch) is an elongate, triangular bone, with a groove for the hyoidean artery near the upper edge of its outer face. The distal ceratohyal (Dch) is rectangular, with a deeply concave lower margin. The groove for the hyoidean artery runs just above the centre of the outer face of the bone, and is interrupted by an elongate, oval fenestra. There are two hypohyals. The lower hypohyal (Hhl, Fig. 9) is a large, square bone, articulating with its fellow by a facet at the antero-ventral corner. The upper hypohyal (Hhu, Fig. 9) is rarely clearly visible, evidently because it was small and inclined medially so that it is usually crushed between the large lower hypohyals. The foramen of the hyoidean artery lies entirely within the upper hypohyal. There is no sign of an ossified basihyal. In front of the hypohyals there is a heart-shaped dermal plate bearing small marginal teeth (Bht, Fig. 9) which was probably underlain by an unossified basihyal. There is a very long, slender urohyal (Uh, Fig. 9) extending from the hypohyals back to the cleithral symphysis. The head of the urohyal is forked and its anterior half is rod-like. The posterior half of the bone bears a pair of broad, ventro-lateral laminae whose anterior margins curve forwards in a characteristic way (Fig. 9).

There are eleven branchiostegals (Brr, Fig. 9 ; Fig. 32), seven inserted on the distal ceratohyal, one on the line of junction between the distal and proximal ceratohyals, and three on the proximal ceratohyal. The first six rays are thin and hair-like, the next three broader and acinaciform (McAllister 1968), the last two spathiform and curved upwards distally.

(viii) *Branchial arches.* Fragments of the gill arch skeleton are visible in several specimens, notably P.13876, but they show nothing remarkable and the pharyngeals are not visible. The first gill arch bore very long, toothless, close-packed gill-rakers, reaching 2.5 mm. in length in a fish of 17 mm. head length.

(ix) *Opercular bones.* The preopercular (Pop, Figs. 6, 9) is expanded at the angle and has the horizontal limb only a little shorter than the vertical limb. The vertical limb ends close below the pterotic and there is no suprapreopercular. The preopercular sensory canal ran in a closed tube lying close to the anterior edge of the bone. One or two small, postero-dorsally directed branches leave this tube above the angle, while at and below the angle there are four or five branches. The upper-

most of these branches has a short intraosseous portion opening into a long groove running postero-ventrally, the next branch has a larger bone-enclosed portion opening into a shorter groove, and the remaining two or three branches open ventrally, close to the main canal. The anterior part of the canal ran in a groove which is open ventrally.

The opercular (Op, Figs. 6, 9) has an excavated antero-dorsal margin and a rounded upper edge, extending up to the post-temporal. The subopercular (Sop, Figs. 6, 9) is moderately large, with the usual spike at its antero-dorsal corner. The upper edge of the subopercular lies at about 65° to the anterior edge of the opercular. The interopercular (Iop, Figs. 6, 9) is a very long triangular bone, largely concealed by the preopercular. Apart from a few shallow, radiating grooves on the opercular, there is no ornament on the opercular bones, and they are not covered by scales.

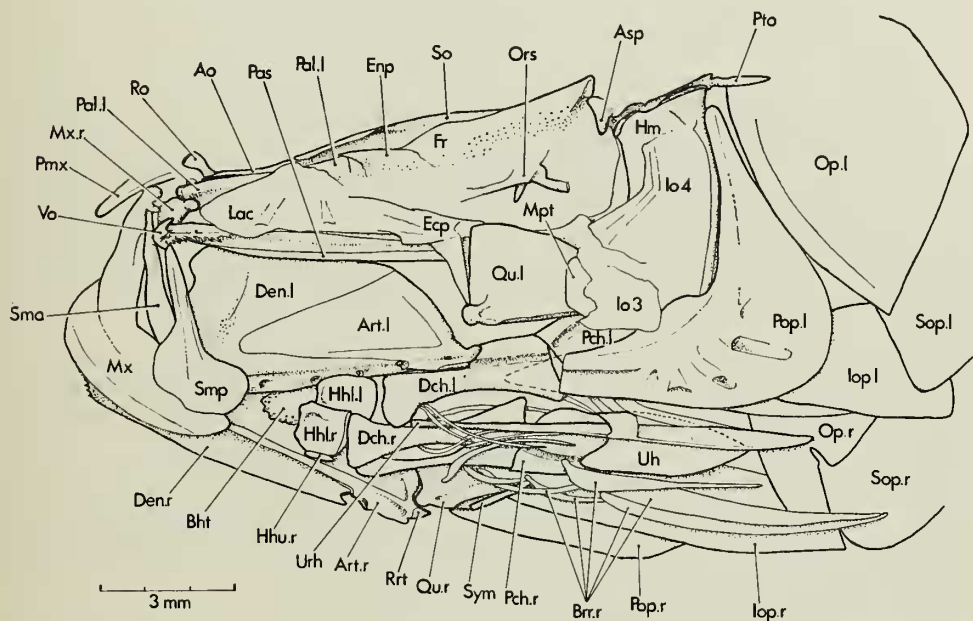


FIG. 9. *Gaudryella gaudryi* (Pictet & Humbert). Skull crushed in ventro-lateral aspect, as preserved in P.9991, Hajula, Lebanon. The suffixes 'r' and 'l' denote bones of the right and left side, explanation of other abbreviations p. 296.

(x) *Vertebral column.* There are 41-44 vertebrae (mean of 13 specimens is 43.0) and a free second ural centrum (Fig. 33). Normally there are fifteen caudal vertebrae (range 13-16) and twenty-eight abdominals. The centra are slightly longer than high, and are well ossified, with longitudinally ridged lateral surfaces but with a narrow, open notochordal canal. The neural and haemal arches of the caudal vertebrae and the neural arches and parapophyses of the posterior abdominal vertebrae are fused to the centra, but on the first twelve to fifteen vertebrae the neural arches and the large, triangular parapophyses are autogenous. The neural arches

and spines are paired structures on the first four or five vertebrae, but are fused in the mid-line on the remaining vertebrae. There are seven or eight rod-like supraneurals above the anterior vertebrae. The epineurals are outgrowths of the neural arches on the first eight to ten vertebrae, but are separate ossifications on succeeding vertebrae. The last epineural is in the region of the last abdominal vertebra. The epineurals are simple rods, with no bifurcation. There are no pleural ribs on the first two vertebrae, but the first centrum has a pair of short, postero-lateral processes, probably for the insertion of Baudelot's ligament. The remaining abdominal vertebrae bear stout pleural ribs extending to the ventral margin of the trunk. The heads of the ribs are expanded antero-ventrally and postero-dorsally, and articulate with similarly elongated facets on the parapophyses. The parapophyses of the last six or seven abdominal vertebrae increase in length progressively while the ribs decrease in size. Rod-like epipleurals articulate with the parapophyses of the abdominal vertebrae and sometimes extend to the first two or three caudal vertebrae. The neural and haemal spines of pre-ural vertebrae 3-7 increase progressively in length and thickness. The caudal skeleton is described below, together with the caudal fin.

(xi) *Pectoral girdle and fin.* The supratemporal (Stt, Fig. 6) is a flimsy, triangular bone which is always more or less crushed into the opening of the post-temporal fossa: the bone overlies the parietal and epiotic medially and covers the opening of the post-temporal fossa laterally. The lateral line canal from the post-temporal entered the supratemporal posteriorly and bifurcated near its anterior margin, a short antero-lateral branch transmitting the temporal canal to the pterotic, and a longer medial branch transmitting the supratemporal commissure to the transverse groove on the parietal.

The post-temporal (Ptt ; Fig. 11A) has a short, stout ventral limb articulating with the intercalar and a long, curved dorsal limb extending antero-medially and almost meeting its fellow in the mid-line above the supraoccipital. Probably the post-temporal was attached to the epiotic by a ligament. The lateral line canal penetrated the bone near its ventral margin, giving off two branches dorsally en route.

The supracleithrum (Scl, Fig. 10) is long and broad, arching forwards from its contact with the lateral face of the cleithrum to articulate with the postero-ventral part of the post-temporal. The lateral line canal from the anterior lateral line scale passed obliquely up through the bone into the post-temporal.

The cleithrum (Cl ; Figs. 10, 11) has a long upper part, above the fin insertion, with a very broad, triangular posterior plate, and a short ventral part, arching forwards to the cleithral symphysis. The medial edge of the central portion of the bone is turned inwards to form the hind margin of the gill chamber, as usual. There are two postcleithra, the upper a rather large, plate-like bone lying medial to the posterior plate of the cleithrum, the lower (Pcv, Fig. 10) a flattened rod passing postero-ventrally from the lower edge of the upper.

The endoskeletal pectoral girdle consists of three bones, scapula, coracoid and mesocoracoid. The scapula (Sca ; Fig. 11B) has a large scapular foramen near its antero-ventral margin, a postero-dorsal process which is applied to the medial face of the cleithrum, and the usual saddle-shaped facet for the first pectoral fin-ray. The coracoid (Cor, Fig. 10) is rather large, with a deep anterior process passing forwards to

the tip of the cleithrum, leaving a triangular fenestra between this contact and the upper attachment of the coracoid to the cleithrum. A short antero-dorsal process of the coracoid joins with a similar process of the scapula in receiving the ventral end of the mesocoracoid. Just below this process on the medial face of the coracoid

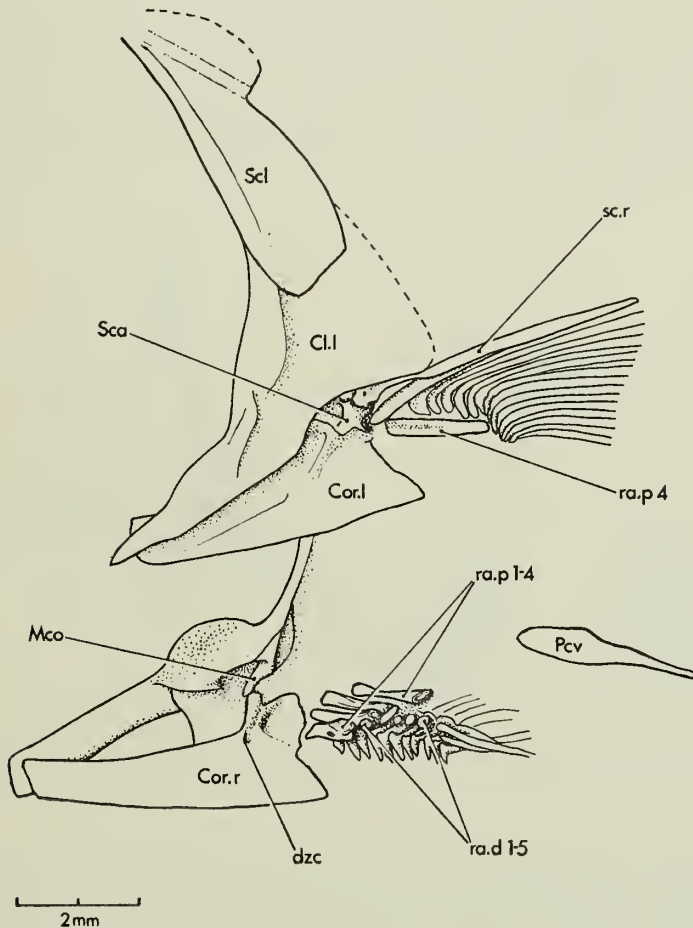


FIG. 10. *Gaudryella gaudryi* (Pictet & Humbert). Pectoral girdle as preserved in P.9991, Hajula, Lebanon. Above is the left girdle in lateral view, below the right girdle in medial view. *dzc*, diazonal canal in coracoid; *Mco*, mesocoracoid; *Pcv*, ventral postcleithrum; *ra.d* 1-5, distal pectoral radials; *ra.p* 1-4, proximal pectoral radials; *sc.r*, scale-like upper hemitrich of first pectoral ray; suffixes 'r' and 'l', bones of right and left side; other abbreviations p. 296.

there is a diazonal canal (*dzc*, Fig. 10) leading antero-ventrally. The mesocoracoid (*Mco*, Fig. 10) is an arched strut extending down from its expanded attachment to the cleithrum to meet the scapula and coracoid.

There are four proximal pectoral radials (ra. p. 1-4, Fig. 10). The uppermost is short, of complex form, and pierced by a canal. The lower three radials increase progressively in length and take the form of compressed rods, broader at each end. There is a series of distal pectoral radials, small, nodular ossifications lying between the bases of the hemitrachs of the upper fin-rays. P.9991 shows five distal radials (ra. d 1-5, Fig. 10), while in P.48048 and AM 3783 there appear to be at least six.

The pectoral fin contains fifteen or sixteen rays (more commonly 16), all segmented distally. The longest rays of the fin, the third and fourth, are equal in length to eight vertebrae. The first ray, which articulates directly with the scapula, is very asymmetrical, with its upper hemitrach modified into a thin, scale-like plate (sc.r, Fig. 10), segmented distally.

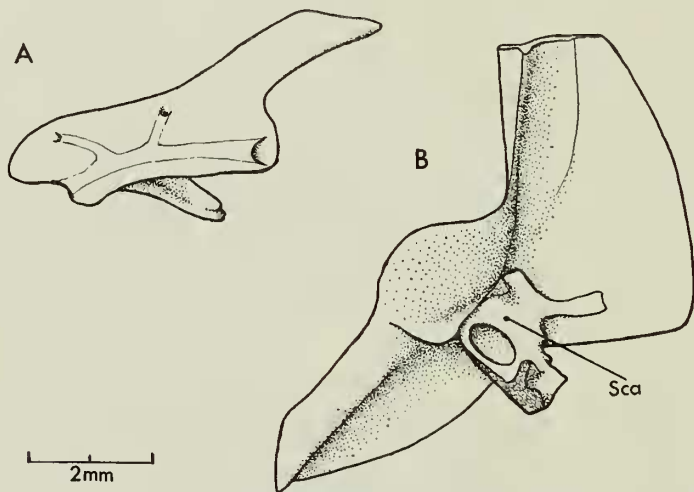


FIG. 11. *Gaudryella gaudryi* (Pictet & Humbert). A, isolated right post-temporal, P.51255, in lateral view. B, ventral part of isolated right cleithrum and scapula, P.51256, in medial view. From different individuals, Hajula, Lebanon.

(xii) *Pelvic girdle and fin.* The pelvic girdle lies below the middle part of the dorsal fin and the pelvic fins originate below the last rays of the dorsal, at about the twenty-first vertebrae. Each pelvic bone (Fig. 12) consists of an antero-medially inclined shaft of thin, membranous bone, and a medial process of thicker, endochondral bone, both these portions meeting their antimeres in the mid-line. The pelvic bone has a complex articular surface at its postero-lateral corner. Above this surface there is a curved, postero-lateral process of dense bone, arising on the dorsal surface of the pelvic bone and projecting alongside the base of the upper hemitrach of the first pelvic ray (p. sp, Fig. 12) : this process appears to represent the pelvic splint, here fused with the pelvic bone. Only a single ossified pelvic radial has been seen (p.ra, Fig. 12C), projecting posteriorly medial to the base of the innermost fin-ray (cf. Gosline, Marshall & Mead 1966, fig. 3 ; Weitzman 1967b, figs. 5, 6, 16). Other pelvic radials may be present, obscured by the bases of the fin-rays.

The pelvic fin contains 12 (3 of 8 specimens) or 13 (5 of 8 specimens) rays, all segmented distally. As noted above, the short, hooked splint is fused with the pelvic girdle. The pelvic fin is shorter than the pectoral, the longest rays being equal in length to about five vertebrae.

(xiii) *Dorsal and anal fins*. The dorsal fin (Fig. 33) lies at the mid-point of the back of the fish and occupies a length of about six vertebrae. The fin contains twelve rays supported by eleven radials. A twelfth radial is present, but carries no fin-ray, only a posterior expansion of the head. The first radial has a stout anterior process from its head. Except for the first three or four, the radials have separate ossified middle segments. The shaft of the first radial ends above the thirteenth or fourteenth vertebra. The dorsal fin-rays are all segmented distally and all except the first two are branched. The longest fin-ray, the third, is equal in length to about eight vertebrae, a little less than the maximum depth of the trunk.

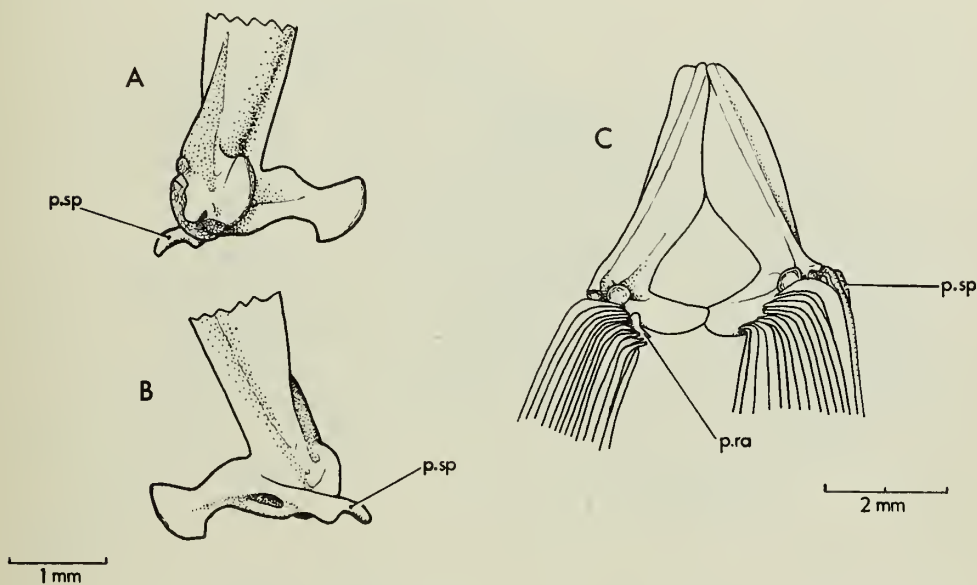


FIG. 12. *Gaudryella gaudryi* (Pictet & Humbert). A,B, posterior part of isolated right pelvic bone, P.51257, in ventral (A) and dorsal (B) view. C, pelvic girdle and fins in ventral view, as preserved in P.9991. Both from Hajula, Lebanon. *p.ra*, inner pelvic radial; *p.sp*, pelvic splint.

The anal (Fig. 33) is small and remote, originating below the tenth pre-ural vertebra and occupying a length of four vertebrae. The fin contains nine rays supported by eight radials. The fin-rays are slender and short, the longest being about equal to the base length of the fin. All are segmented distally and all but the first two are branched. The first radial ends proximally close to the haemal spine of the third caudal vertebra.

(xiv) *Caudal skeleton and fin.* The caudal skeleton (Figs. 13, 14) is considerably specialised by fusion of parts. The neural and haemal spines of the third and fourth pre-ural vertebrae are long and slightly expanded distally: the haemal spine of PU₃ is autogenous and has a small anterior lamella near the base. The neural spine of PU₃ also has a small anterior lamella (Fig. 14). In some specimens the foremost procurent caudal rays articulate with the neural spine of PU₃ above and the haemal spine of PU₄ below, in others they articulate with the first epural above and the haemal spine of PU₃ below. PU₂ has a leaf-like neural spine (npu₂), about half as long as its predecessor, as in *Elops*, *Aulopus* and *Nematonotus* (Patterson 1968b: 84), and a long, stout haemal spine with anterior and posterior lamellar expansions, the anterior one touching the preceding haemal spine proximally, the posterior one fitting against a similar expansion from the parhypural. The haemal arch of PU₂

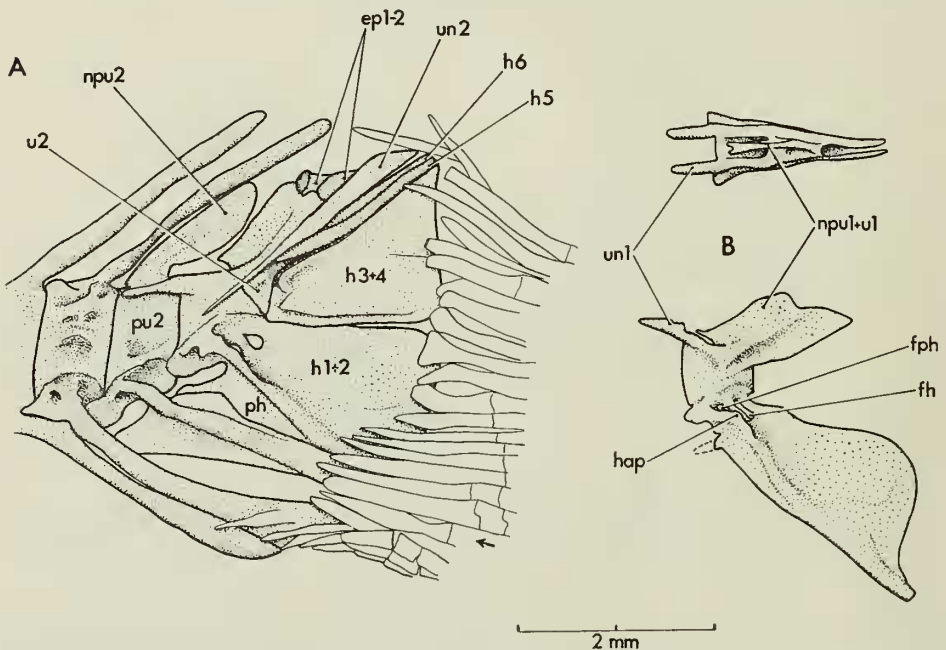


FIG. 13. *Gaudryella gaudryi* (Pictet & Humbert). A, caudal skeleton as preserved in P.9991; an arrow marks the lowermost (unbranched) principal fin-ray. B, isolated compound centrum and attached structures, P.51258, in dorsal (above) and left lateral view. Both from Hajula, Lebanon. Explanation of abbreviations p. 296.

is certainly autogenous, the neural spine is probably also autogenous, but the suture between arch and centrum is always covered by the first uroneural. The first pre-ural and ural centra are fused and form part of a complex structure (Fig. 13B) into which are also fused the parhypural (ph), the two lower hypurals (h₁₊₂) and the stegural. A line of fusion is often visible between the compound centrum and the combined parhypural and lower hypurals: evidently this fusion occurred during

ontogeny. Similarly, there may be a line of fusion between the parhypural and the first hypural, but the first and second hypurals are indistinguishably fused, only the hypural foramen (fh, Fig. 13B : Monod 1968 : 640) indicating that the second hypural is incorporated. The parhypural has a rudimentary hypurapophysis (hap), and is a little longer than the first hypural but much more slender. The stegurals have paired ventral parts, representing the first uroneural (un1), extending forwards and back from the compound centrum, and a median dorsal crest arching forwards over the narrow neural canal and fitting against the second pre-ural neural spine, presumably representing the neural arches of the first ural and pre-ural centra (npur + ur).

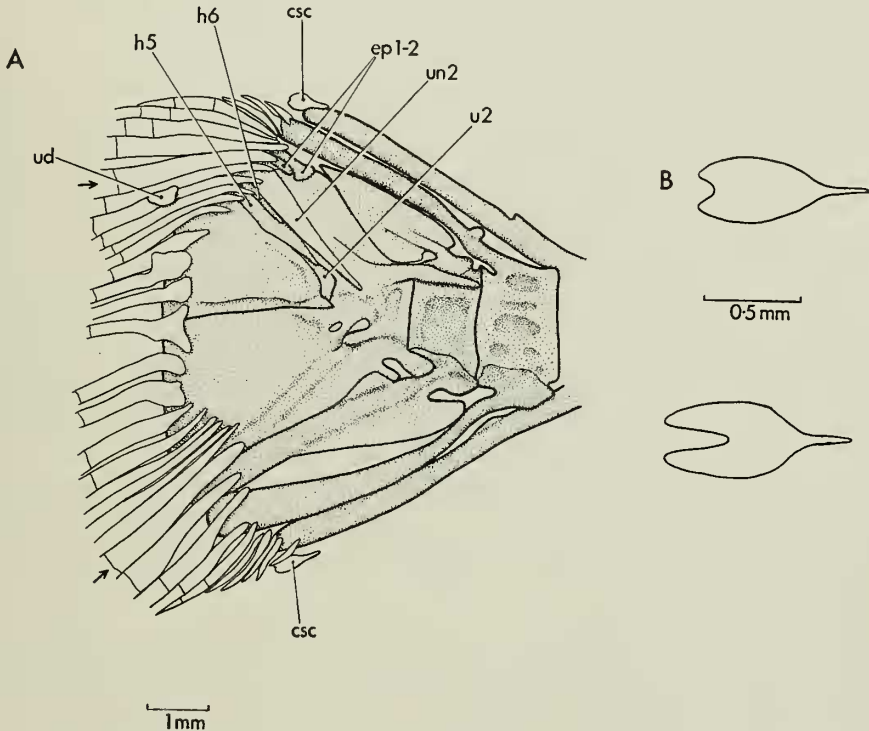


FIG. 14. *Gaudryella gaudryi* (Pictet & Humbert). A, caudal skeleton as preserved in AM 5579 ; arrows mark the outermost (unbranched) principal fin-rays. B, upper (above) and lower caudal scutes, restored on the basis of AM 5568. Both from Hajula, Lebanon. Explanation of abbreviations p. 296.

The first uroneural was evidently forked proximally (cf. *Humbertia*, Figs. 26, 27) as in *Elops* and *Nematonotus*, and is therefore probably compound in origin (Patterson 1968a : 226). The upper fork extends forwards across the second pre-ural centrum while the ventral fork is fused into the compound centrum. Posteriorly the stegurals extend back as a broad, paired flange, with a lateral groove housing the second

uroneural. The second uroneural (un2) is slender and pointed anteriorly, where it fits in the groove on the stegural, and broad posteriorly. There is no third uroneural.

There is a small independent second ural centrum (u2), supporting the upper hypurals. There appear to be four upper hypurals, the third and fourth (h3+4) very broad and fused together, but often with a partial suture suggesting that fusion occurred during ontogeny, the fifth and sixth (h5, h6) very slender and separate. The fifth and sixth hypurals sometimes give the impression of uroneurals, since their proximal ends extend forwards alongside the second uroneural in slender points, that of the fifth hypural lying dorso-lateral to the second ural centrum, as in *Esox* (Monod 1968 : 355), *Humbertia* (p. 248), *Argentina* (Fig. 38) and osmerids (Fig. 43). There are two epurals (ep 1-2) above the posterior part of the stegural. The first epural is broad and expanded proximally, the second is slender.

The forked caudal fin contains nineteen principal rays with seventeen branched (nine in the upper lobe, eight in the lower). There are five to seven upper procurent rays, the first two or three unsegmented, and seven to nine lower procurent rays, the first two to four unsegmented. Close to the foremost procurent fin-ray above and below there is a very small, leaf-shaped caudal scute (csc ; Fig. 14B). There is a single urodermal (ud, Fig. 14A), lying on the second fin-ray below the uppermost principal ray, well clear of the uroneurals.

(xv) *Squamation*. The scales are very thin and are always poorly preserved. They are cycloid, with continuous, well separated circuli, and contain no bone-cell spaces. The scales are large, the lateral line scales being equal in depth to almost a quarter of the depth of the trunk, and there can only have been six to eight scales in a transverse series on the trunk. There is a broad, continuous lateral line, the number of lateral line scales being approximately equal to the number of vertebrae. There are no scales on the cheek or operculum, or on the bases of the fins.

(xvi) *Soft anatomy*. In most of the specimens from Hajula the musculature is preserved as a cream coloured phosphatic mass. Myocommata are occasionally visible within this mass. The course of the gut is indicated by its fossilised contents, showing that the anus lay close in front of the origin of the anal fin, below the third or fourth caudal vertebra.

There is no convincing evidence of an adipose fin, despite attempts to discover one by various stains, ultraviolet light, etc. But even in the myctophoids from these deposits, which surely had adipose fins and which are usually preserved in lateral view, the fin is never clearly demonstrable.

In some specimens the pigment of the retina is preserved, indicating that the eye was large, filling the orbit and having a diameter about equal to one-third of the braincase length. The same specimens show the pattern of chromatophores on the trunk, demonstrating that the back was uniformly pigmented and the belly was white.

As noted above, the scales consist of acellular bone, and this is true of the rest of the skeleton, dermal and endochondral, except for certain areas, mostly close to articular surfaces, where the bone is densely cellular, containing small, rounded chondrocyte-like spaces, without canaliculi. These cellular areas include the cranial condyle and palatine facet of the maxilla, the head of the vomer and palatine, the

antero-dorsal corner of the coronoid process of the dentary, the condyle of the quadrate, the antero-ventral corner of the lower hypohyal and the glenoid region of the scapula and coracoid.

Humbertia gen. nov.

DIAGNOSIS. Small, slender, round-bodied salmoniform fishes ; parietals in contact medially and bearing the supratemporal commissure, post-temporal fossa roofed ; nasals long and tubular ; rostral not distinct from mesethmoid, which is flat and shield-like anteriorly with paired splints passing back below the frontals ; vomer broad, toothless, with a long posterior process, parasphenoid toothless, with a rudimentary basipterygoid process ; occipital condyle formed by basioccipital only, intercalar small, wall of otolith chamber somewhat inflated, basisphenoid and orbitosphenoid present, sclerotic ossified ; dermosphenotic and supraorbital large, circumorbital ring of bones almost complete, antorbital, lachrymal and four infra-orbitals present, posterior infraorbitals extending to preopercular ; hyomandibular vertical, single-headed, metapterygoid not reduced, quadrate condyle below centre of orbit, no pterygoid teeth, a single row of small palatine teeth ; gape small, premaxilla about 40% as long as maxilla, toothed and with rudimentary ascending and articular processes, maxilla toothed, not extending to middle of orbit, two mobile supramaxillae ; mandible with long, high coronoid process, dentary with short, steeply ascending oral border bearing a few small teeth near the symphysis followed by a short diastema and a series of blade-like, serrated teeth, pocket for Meckel's cartilage on inner face of dentary minute ; distal ceratohyal perforate, distal and proximal ceratohyals sutured together, basihyal very small or unossified, toothless ; seven or eight branchiostegals, the posterior ones spathiform and crescentic ; toothless dermal plates fused with second and third basibranchials, upper and lower pharyngeal teeth conical, third hypobranchial long, fourth epibranchial deep and perforated by an efferent arterial foramen, short, toothless gill-rakers on gill arches ; no supra-preopercular, subopercular about as large as opercular ; about 38 vertebrae, 15 caudal, anterior neural arches and parapophyses autogenous, simple epineurals and epipleurals on abdominal vertebrae, anterior epineurals fused to neural arches ; mesocoracoid, two postcleithra and several distal pectoral radials present ; pelvics inserted below posterior part of dorsal, 12-13 rayed, pelvic splint present ; dorsal fin short, lying just in front of mid-point of trunk, anal fin small and remote ; PU2 with short, leaf-like neural spine, lamellar expansions on neural spines of PU3-5 and haemal spines of PU2-3 ; PU1 and U1 fused, U2 separate, six autogenous hypurals ; stegural autogenous and forked proximally, second and third uroneurals present, third lying lateral to second ; three epurals ; caudal fin forked, 19-rayed, one urodermal and large caudal scutes present ; scales large, cycloid, not extending on to skull or fins, lateral line complete ; skeleton mainly acellular.

TYPE (and only) SPECIES. *Humbertia operta* sp. nov.

Humbertia operta gen. et sp. nov.

Pl. 1, fig. 3 ; Pl. 2, fig. 2 ; Pl. 3, fig. 1 ; Pl. 4, fig. 2 ; Pl. 5 ; Figs. 15-27, 30-33

DIAGNOSIS. *Humbertia* reaching about 115 mm. in standard length ; mean proportions (as % standard length) : total length 119, head length 30.5, trunk depth 19.5, predorsal length 41.5, preanal length 82, prepelvic length 56 ; 36-39 vertebrae, mean 38, 15 caudal ; D iii, 11 ; A ii, 6 ; P 16-17 ; V 12-13 ; C v-viii, I, 9, 8, I, v-viii ; eight scales in a transverse series on the trunk, about 40 along the lateral line.

HOLOTYPE. BM(NH) P.48218/9 (Pl. 3, fig. 1 ; Fig. 26), a fish in counterpart from Hakel, the part a transfer preparation.

HORIZON AND LOCALITIES. Middle Cenomanian, Hakel and Hajula, Lebanon.

MATERIAL. The holotype and P.51259 from Hakel, and numerous specimens from Hajula in the BM(NH) and the American Museum of Natural History, especially the following transfer preparations : P.51243, P.51260 (Pl. 4, fig. 2), P.51261-2, P.51263 (Fig. 20), AM 3783 (Figs. 17B, 18), AM 4115 (Pl. 5, fig. 1 ; Fig. 25), AM 4411 (Pl. 5, fig. 2 ; Fig. 19), AM 4580 (Fig. 15A), AM 4590 (Pl. 2, fig. 2 ; Fig. 21), AM 5563 (Fig. 15B), AM 5564 (Fig. 27), AM 5565, AM 5567, AM 5571, AM 5574 (Fig. 15C), AM 5579 ; and the following isolated bones or parts of the skeleton : P.51264 (Fig. 16), P.51265-6 (Fig. 17), P.51267-9 (Fig. 22), P.51270-2 (Fig. 23), P.51273 (Fig. 24).

DESCRIPTION. (i) *General features.* *Humbertia operta* is similar to *Gaudryella gaudryi* in general appearance and it is often very difficult to differentiate the two in unprepared material (Pl. 3). The largest individual, AM 4580, is incomplete posteriorly but must have been about 115 mm. in standard length, almost 30% longer than the largest *Gaudryella* (90 mm.). But, as in *Gaudryella*, such large specimens are unusual and the modal standard length is 60-70 mm. The fish must have been uncompressed, even slightly depressed, since only very occasional specimens are preserved in lateral view (two out of about 50) while dorso-ventral preservation of the head is not uncommon, and the trunk of dorso-ventrally crushed specimens appears broader than in those laterally crushed. The dimensions of nine specimens are given in Table 2 : as in *Gaudryella* the variability in some of these proportions is mainly due to inaccuracies caused by twisting and distortion of the fishes during fossilisation. In comparison with *Gaudryella gaudryi* (Table 1) the caudal fin and head are slightly longer while the predorsal, preanal and prepelvic lengths are slightly smaller, but these differences between the means fall well within the range of variation of the two sets of specimens. The apparent greater depth of the trunk in *H. operta* is perhaps due only to overestimation of the depth of the trunk in most of the listed specimens (only AM 3808 and P.9147 are laterally crushed). Table 2 suggests that in *Humbertia* there was a small relative decrease in head length and prepelvic length with increasing standard length, although this is partially due to the influence of the very small P.51274, a rather distorted fish.

(ii) *Skull roof and braincase.* The skull roof is partially shown in Figs. 15, 19 and is restored in Fig. 30. It differs from that of *Gaudryella* in having a shorter, broader, postorbital division and shorter, broader snout. As in *Gaudryella*, the skull roof is flat apart from the raised tubes containing the sensory canals, but in larger specimens

there are a few ridges radiating from the centre of ossification of the frontal and supraorbital. The supraoccipital (Soc) and epiotics (Epo) are very like those of *Gaudryella*. The parietals (Pa) are always rather poorly preserved. They are shorter and broader than in *Gaudryella*, but as in the latter they are in contact medially, meet the pterotics laterally, roofing the post-temporal fossa, and join the epiotics in digitate sutures postero-laterally. The transverse groove across the parietal which contained the supratemporal commissure is longer, more deeply incised and closer to the posterior edge of the bone than in *Gaudryella*, and shows no sign of division into two parts.

TABLE 2

Proportional measurements of nine specimens of *Humbertia operta*
as % standard length

Specimen	Standard length, mm.	Total length	Head length	Trunk depth	Predorsal length	Preanal length	Prepelvic length
P.51274 (Hajula)	23	118	35	15	41	78	59
P.51275 (Hajula)	51	120	30	20	41	82	57
P.51260 (Hajula)	51	118	31	20	41	82	56
AM 4411 (Hajula)	59	119	31	25	40	80	54
AM 4414 (Hajula)	60	118	32	20	42	84	61
AM 3808 (Hajula)	64	119	33	17	45	86	58
P.9147 (Hajula)	71	118	29	18.5	44	83	53
P.48218 (Hakel)	87	122	27.5	21	41.5	81	52
AM 5570 (Hajula)	110	—	26	18	39	84	52
Mean	—	119	30.5	19.5	41.5	82	56

The frontals (Fr) differ from those of *Gaudryella* principally in having the parietal branch of the supraorbital sensory canal longer and broader, the epiphyseal branch shorter and more posteriorly directed, and in having laminar anterior ends which extend forward to the tip of the snout, dorsal to the mesethmoid. The nasals (Na, Figs. 15, 19) are slender and laterally placed, as in *Gaudryella*, but are tubular and much longer than in the latter.

The mesethmoid (Mes, Figs. 15, 19 ; Fig. 16) is very different from that of *Gaudryella*. There is no separate rostral, this dermal element apparently having fused completely with the underlying endo- and perichondral ossification to produce a compound mesethmoid. The dorsal part of the bone is dense and probably mainly dermal in origin. Its upper surface is almost flat, with a broad, shield-shaped anterior part

and a narrower posterior part ending in a pair of delicate splints which extend back beneath the frontals. At the front of the dorsal surface of the mesethmoid there is a median depression which probably housed ligaments to the ascending processes of the premaxillae. On the underside of the bone there is a pair of vertical laminae of perichondral bone (equivalent to the capsular ethmoids of Weitzman) which splay out anteriorly and end at the widest part of the bone. In front of this point, below the broad anterior part of the bone, there are only traces of granular endochondral bone, and the foremost part of the ethmoid cartilage was apparently unossified. The vertical laminae of perichondral bone are joined ventrally by a horizontal lamina, equivalent to the ventral ethmoid of Weitzman.

The lateral ethmoids (Le, Fig. 21) are quite heavily ossified but are normally hidden below the large supraorbital.

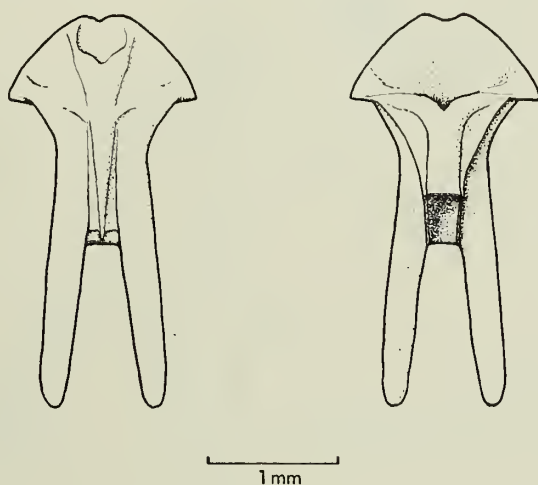


FIG. 16. *Humbertia aperta* gen. & sp. nov. Isolated mesethmoid in dorsal (left) and ventral view. Restoration based on P.51264, Hajula, Lebanon.

The vomer (Vo, Figs. 15B, 19 : Fig. 17A) has a broad, rounded head and a long, tapering posterior process extending back below the parasphenoid to the level of the centre of the orbit. The bone is toothless, the underside of its head bearing only a median depression and a pair of lateral depressions into which the palatines fit. On the dorsal surface of the head of the vomer there is a pair of antero-laterally directed facets with which the maxillary heads articulate, and a median knob presenting a pair of articular surfaces for the heads of the premaxillae. The parasphenoid (Pas ; Fig. 17B) is toothless, as in *Gaudryella*. At the hind edge of the orbit the parasphenoid broadens abruptly into a pair of short lateral processes (bpt) which are penetrated by the foramen of the efferent pseudobranchial artery (epsa). These processes appear to be rudimentary basipterygoid processes, homologous with those of osteoglossoids, ichthyodectids (Bardack 1965), the clupeoid *Diplomystus* (Patterson 1967b) and more primitive actinopterygians. Whether in *Humbertia* the

basipterygoid processes articulated with the palate is not possible to discover, but in skulls preserved in lateral view (Fig. 19) the metapterygoid lies very close to the basipterygoid process and such an articulation is likely. Between the bases of the basipterygoid processes there is a very small bucco-hypophysial canal (bhc), patent in the single specimen where both sides of the parasphenoid are visible. The ascending processes of the parasphenoid are long and high, forming the lower part of the somewhat inflated otolith chambers. The ascending process is penetrated by the internal carotid in the usual way (fica). Posteriorly the parasphenoid ends just in front of the occipital condyle (Fig. 18). Probably the myodome opened posteriorly, as in *Gaudryella*.

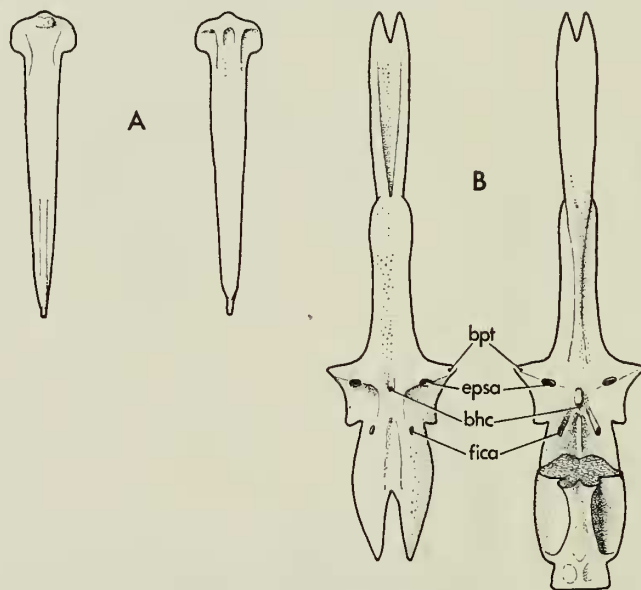


FIG. 17. *Humbertia aperta* gen. & sp. nov. A, isolated vomer, P.51265, in dorsal (left) and ventral view. B, parasphenoid in ventral view (left) and in dorsal view with basioccipital in position (right), restorations based on P.51266 and AM 3783. All from Hajula, Lebanon. bhc, bucco-hypophysial canal; explanation of other abbreviations p. 296.

The endocranium is partially visible in several transfer preparations, and parts of the otic and occipital regions are preserved in two dissociated individuals on AM 3783 (Fig. 18). In comparison with *Gaudryella* the endocranium is rather poorly ossified, with cartilagenous interspaces between many of the bones so that they become more or less disarticulated during fossilisation: this break-up of the underlying endocranium is responsible for the poor preservation of the posterior part of the skull roof in this species. As in *Gaudryella*, the occipital condyle is formed by the basioccipital (Boc) alone. The wall of the saccular recess is more inflated than in *Gaudryella* but there is no fenestra at the junction of the prootic (Pro), exoccipital (Exo) and basioccipital. There is some indication of a shallow sub-temporal fossa in the single

specimen showing part of this region, but the intercalar (Ic) appears to be small, with no anterior extension towards the fossa, though again the intercalar is only visible in one specimen and may be incomplete. As in *Gaudryella*, there is no evidence of any association between the ear and the swimbladder. The trigemino-facialis chamber has a lateral opening for the hyomandibular nerve (VII hm) and a rather long jugular canal leading back and opening near the hind edge of the prootic (ptfc). A basisphenoid is present, with a stout pedicel extending down to the parasphenoid.

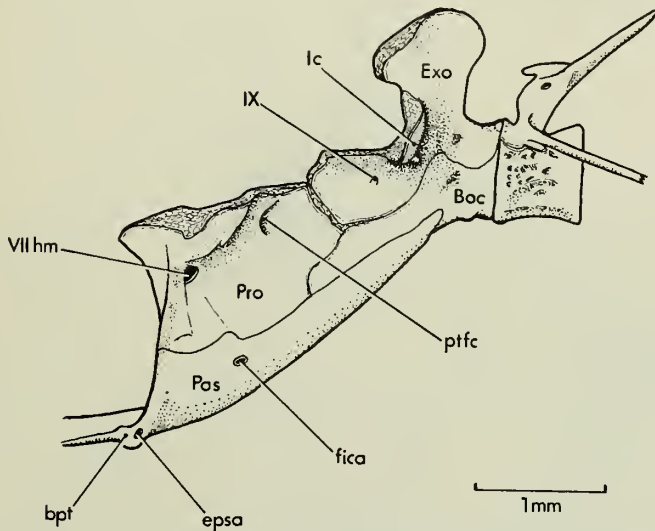


FIG. 18. *Humbertia aperta* gen. & sp. nov. Postero-ventral part of neurocranium and first vertebra in left lateral view, restoration based on AM 3783, Hajula, Lebanon. Explanation of abbreviations p. 296.

The hyomandibular facet is single, but is much constricted at the sphenotic/ptertotic junction, with expanded, cup-like anterior and posterior regions. The autosphenotic (Asp, Figs. 15, 19, 21) has a spine-like postorbital process forming the anterior margin of a rather deep dilatator fossa. The otic nerve emerged in the upper part of the dilatator fossa, through the base of the postorbital process (fofn). The dermal and endochondral pterotic ossifications are fused into a compound pterotic, as in *Gaudryella*. The pterotic (Pto, Figs. 15A, C, 19) is shorter than that of *Gaudryella* but is similar to the latter in most respects, with the same posterior splint, foramen for the supratemporal branch of the vagus (stv, Fig. 15C), deep groove for the exit of the preopercular sensory canal, and open groove carrying the transverse and longitudinal limbs of the temporal sensory canal. But whereas in *Gaudryella* the groove for the sensory canal is formed only by folding inwards of its outer margin (Fig. 3C), in *Humbertia* the inner edge of the groove projects dorso-medially, especially posteriorly, where it forms a pointed process receiving the sensory canal from the supratemporal.

The pterospheonoids (Pts, Fig. 20) are separated by the optic fenestra and there is a large orbitosphenoid (Ors, Fig. 20), closing the fenestra anteriorly, which differs from the orbitosphenoid of *Gaudryella* in lacking a ventral process in front of the fenestra. The sclerotic is ossified (scr, Fig. 19), probably in four pieces.

(iii) *Circumorbital bones*. There are eight circumorbital bones; dermosphenotic, four infraorbitals, lachrymal, antorbital and supraorbital (Fig. 31). As in *Gaudryella* there is no sign of any association between the infraorbital sensory canal and the antorbital or supraorbital.

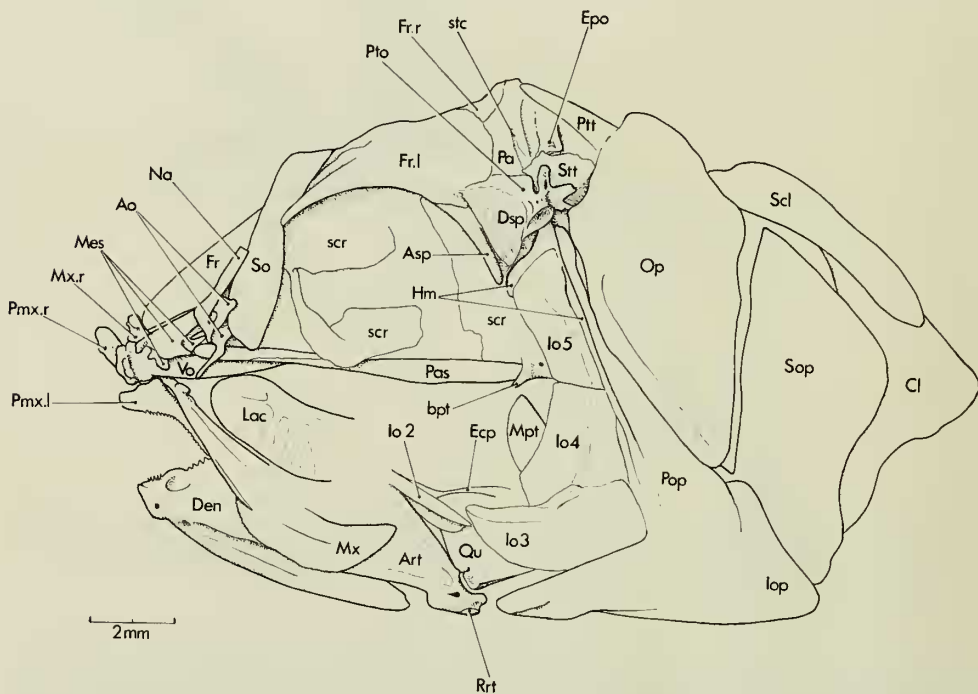


FIG. 19. *Humbertia aperta* gen. & sp. nov. Skull as preserved in AM 4411, Hajula, Lebanon. The ventral part of the preopercular, the supramaxillae and the lachrymal and second infraorbital are damaged in this specimen. The suffixes 'r' and 'l' denote bones of the right and left side, explanation of other abbreviations p. 296.

The supraorbital (So, Figs. 15, 19) is longer and broader than that of *Gaudryella* but is otherwise similar. Posteriorly the supraorbital ends close to the tip of the dermosphenotic so that the circumorbital ring of bones is almost complete. The comma-shaped antorbital (Ao, Figs. 15, 19) is very like that of *Gaudryella* but is a little deeper posteriorly.

As in *Gaudryella*, the infraorbitals are flimsy bones and are never well preserved. The lachrymal (Lac, Figs. 15A, 19-21) is similar in shape to that of *Gaudryella* but is a little deeper, and has only two ventral branches of the sensory canal which are

broader, end closer to the ventral edge of the bone than the three in *Gaudryella*, and are more frequently bifurcated. As in *Gaudryella*, the second infraorbital (Io2, Figs. 19, 21) is slender and about equal to the lachrymal in length. The sensory canal ran near the centre of the bone in a deep groove which is covered over to form a tube for a short distance in the posterior half of the bone. Behind the eye, where there are only two infraorbitals in *Gaudryella*, there are three in *Humbertia*, as in most primitive teleosts. The third infraorbital (Io3, Figs. 19, 20) resembles that of

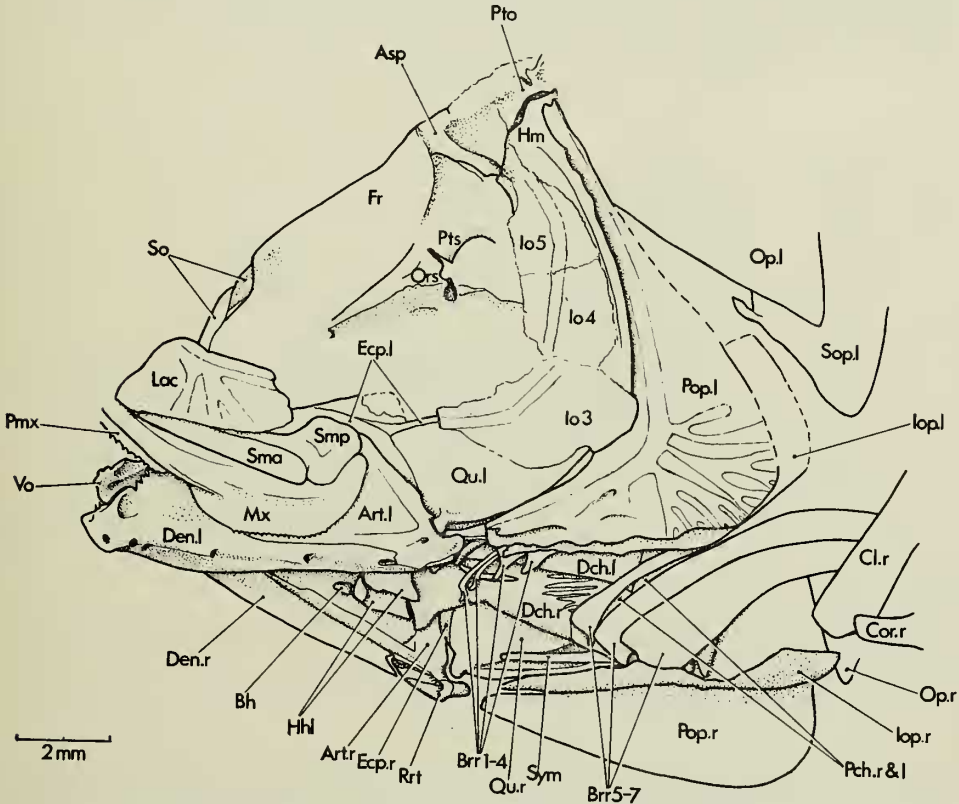


FIG. 20. *Humbertia aperta* gen. & sp. nov. Skull crushed in ventro-lateral aspect, as preserved in P.51263, Hajula, Lebanon. The suffixes 'r' and 'l' denote bones of the right and left side, explanation of other abbreviations p. 296.

Gaudryella in shape, but the sensory canal runs in a channel which is open ventrally, not in a closed tube, and there is no branch in the centre of the bone. The fourth and fifth infraorbitals (Io4, Io5, Figs. 19-21) together appear to be homologous with the fourth of *Gaudryella*. They extend back almost to the preopercular, but are less broad than the single bone in *Gaudryella*. In the fourth infraorbital, as in the third, the sensory canal ran in a channel which is open ventrally; in the fifth the canal ran in a tube.

The dermosphenotic (Dsp, Figs. 15, 19) is elongate and triangular, containing a bone enclosed, triradiate sensory canal, as in *Gaudryella*, but the anterior limb of the bone is longer than in the latter, and the terminal branch of the infraorbital sensory canal within it expands as it passes forwards, and opens at the tip of the bone.

(iv) *Hyopalatine bones*. The hyomandibular (Hm, Figs. 19–21, 25 ; Fig. 22C) is broad and almost vertical. The head of the bone is single but constricted in the centre. As in *Gaudryella* the opercular process lies in the upper third of the bone, opposite the foramen for the hyomandibular trunk on the inner face of the bone. Antero-ventrally there is a deep notch separating an anterior membranous process from the ventral, endochondral part of the bone.

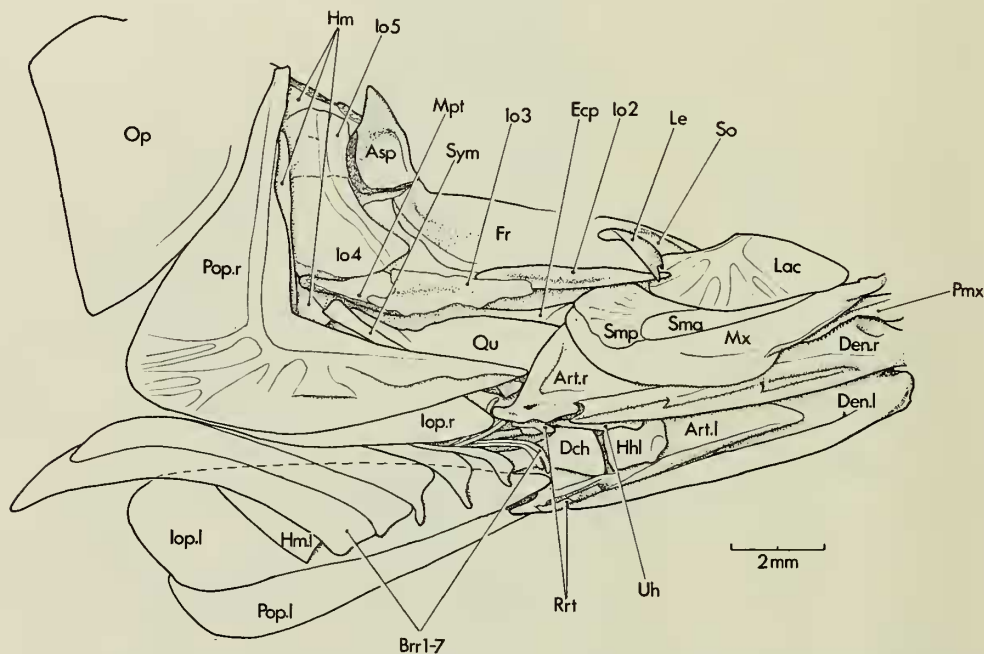


FIG. 21. *Humbertia aperta* gen. & sp. nov. Skull crushed in ventro-lateral aspect, as preserved in AM 4590, Hajula, Lebanon. The left interopercular is drawn in transparency to show the heads of the branchiostegals. The suffixes 'r' and 'l' denote bones of the right and left side, explanation of other abbreviations p. 296.

The metapterygoid (Mpt, Figs. 19, 25) is larger than in *Gaudryella* and is visible in several specimens. In shape it resembles three-quarters of a circle, the upper posterior quadrant being missing. Ventrally it meets the quadrate, postero-dorsally it is overlapped by the hyomandibular, and dorsally it extends up over the medial surface of the endopterygoid, ending in a process which may have articulated with the basiptyergoid process of the parasphenoid (see above).

As in *Gaudryella*, the symplectic (Sym, Figs. 20, 21, 25) is long and the quadrate (Qu, Figs. 19–21, 25) strongly inclined forwards, its condyle lying below the centre of

the orbit. The quadrate resembles that of *Gaudryella* but has a longer posterior process. The ectopterygoid (Ecp, Figs. 19–21) is slender, curved and toothless, as in *Gaudryella*. The endopterygoid is long and also toothless.

The palatine (Pal, Figs. 15, 22B) is straight and rather heavily ossified, as in *Gaudryella*, but differs from the latter in having a row of about ten small, recurved teeth. The head of the palatine has an antero-ventral knob (fvo) which articulates with the vomer, an elongate facet (fme), cartilage capped in life, above this which articulated with the ethmoid, and a smaller, lateral facet (fmnx), also cartilage capped in life, which articulated with the palatine condyle on the maxilla.

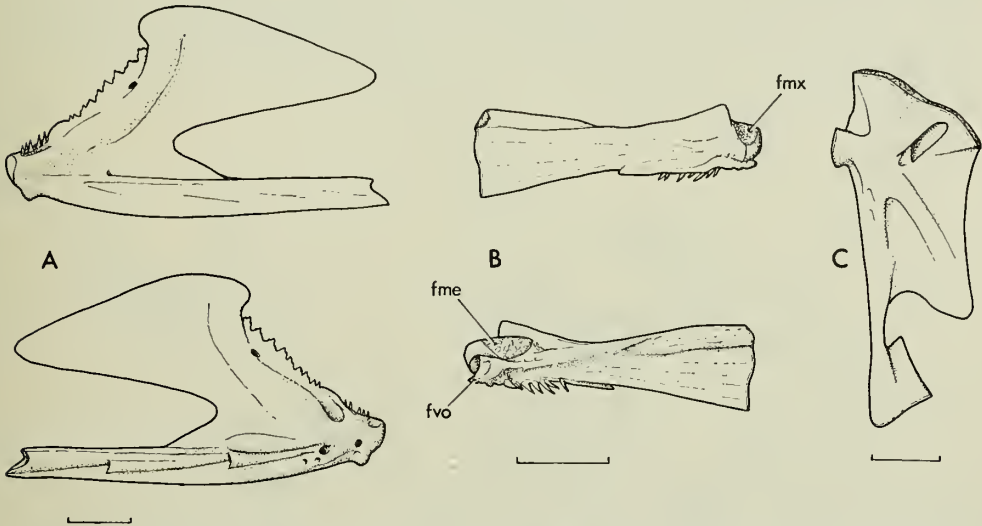


FIG. 22. *Humbertia operta* gen. & sp. nov. A, isolated right dentary, P.51267, in medial (above) and lateral view. B, isolated right palatine, P.51268, in lateral (above) and medial view. C, isolated left hyomandibular, P.51269, in medial view. All from Hajula, Lebanon. Scale 1 mm. fme, fmnx, fvo, facets on palatine articulating with mesethmoid, maxilla and vomer.

(v) *Dermal upper jaw*. As in *Gaudryella*, the upper jaw contains the premaxilla, maxilla and two supramaxillae. The premaxilla (Pmx, Figs. 16, 19, 21; Fig. 23A,B) is equal in length to about 40% of the maxilla compared with about 25% in *Gaudryella*: both the proximal and distal extent of the premaxilla are greater than in *Gaudryella*. The oral border of the bone bears a single series of about twenty small, pointed teeth. Proximally the premaxilla bends medially and met its fellow in the mid-line, forming a blunt snout. This medial part of the premaxilla is toothless and forms a low, rounded ascending process (aspm), separated from the lateral part of the bone by a notch, which must have articulated with the mesethmoid or with a rostral cartilage. Lateral to the notch delimiting the ascending process there is an elongate knob on the inner face of the premaxilla, the articular process (arpm), which fitted in a depression just in front of and below the palatine condyle on the maxilla.

The maxilla (Mx, Figs. 15, 19–21 ; Fig. 23C) is similar in shape and size to that of *Gaudryella*. Proximally there is the usual cranial condyle (hmx) articulating with the mesethmoid, but the flange below the condyle, articulating with the vomer, is reduced in comparison with *Gaudryella*, and has a well marked facet laterally for the articular process of the premaxilla. The palatine condyle (pfmx) is similar to that of *Gaudryella*, but behind it the point of insertion of the palato-maxillary and posterior maxillo-mandibular ligaments is much less prominent than in *Gaudryella*. Above the posterior part of the premaxilla the ventral edge of the maxilla has a curious splint-like appearance, this 'splint' extending a little way back as a lateral flange on the deep, posterior part of the maxilla (Figs. 19–21). Such a 'splint' is not present in *Gaudryella*, or in any other teleost that I know : presumably it marks the insertion of a ligament or band of connective tissue. The oral border of the maxilla bears very small, clustered teeth which extend up the inner face of the bone a little, but are less numerous than in *Gaudryella*.

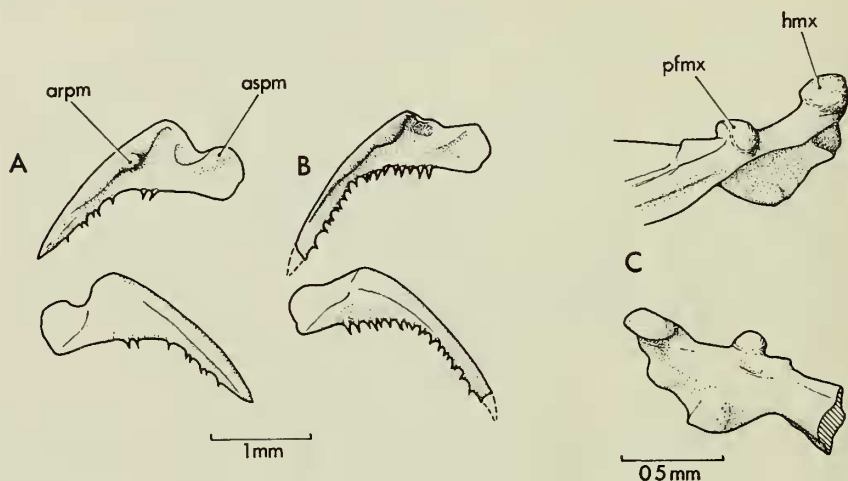


FIG. 23. *Humbertia aperta* gen. & sp. nov. A, B, two isolated left premaxillae, P.51270–1, in internal (above) and external view. C, head of isolated right maxilla, P.51272, in external (above) and internal view. All from Hajula, Lebanon. Explanation of abbreviations p. 296.

The two supramaxillae (Sma, Smp, Figs. 20, 21) are essentially as in *Gaudryella*, except that the body of the posterior supramaxilla is shorter and deeper (cf. Figs. 5, 6, 9). As in *Gaudryella*, the supramaxillae were mobile, being displaced in fossils with the mouth open.

(vi) *Lower jaw*. The mandible is similar in shape to that of *Gaudryella*, with the same short, steeply ascending oral border, and long, high coronoid process. The dentary (Den, Figs. 19–21, 22A, 24, 25) differs from that of *Gaudryella* in having a shallower symphysis, without serrations, and a slightly less steeply ascending oral border which bears six to eight small, recurved teeth close to the symphysis followed

by a short, toothless diastema, and then by a single series of eight to ten blade-like teeth, increasing in size from front to rear, the larger teeth being serrated, with three to five minute cusps. These blade-like teeth are fused with the supporting bone and do not appear to be replaceable, but they have minute pulp cavities, consist of dentine and are true teeth, not serrations of the edge of the dentary. On the inner face of the dentary (Figs. 21, 22A) the pocket for the anterior end of Meckel's cartilage is extremely small, another striking difference from *Gaudryella*.

The angulo-articular (Art, Figs. 19-21, 25) and retroarticular (Rrt) appear to be indistinguishable from those of *Gaudryella*, and the course and distribution of pores and branches of the mandibular sensory canal in the angulo-articular and dentary are also as in *Gaudryella*. There is no sign of a sesamoid articular in the few specimens showing the medial face of the angulo-articular.

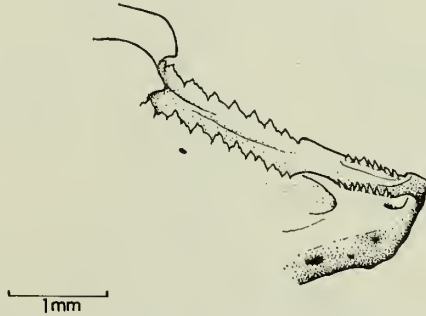


FIG. 24. *Humbertia aperta* gen. & sp. nov. Anterior part of an isolated pair of dentaries, P.51273, in dorsal-lateral view to show the dentition. Hajula, Lebanon.

(vii) *Hyoid arch and branchiostegals*. The hyomandibular is described above, with the palate. The interhyal (Ih, Fig. 24) is short and waisted. The proximal and distal ceratohyals are similar to those of *Gaudryella* (Fig. 32), the proximal ossification (Pch, Figs. 20, 25) elongate and triangular, the distal (Dch, Figs. 20, 21, 25) deep and concave ventrally, both bones with a deep groove for the hyoidean artery on the outer face, the groove interrupted by an oval fenestra in the distal ossification. The main difference from *Gaudryella* is that the two ossifications, separated by cartilage in the latter, are sutured together by long, interdigitating spicules of bone on the inner surface (Fig. 20). The lower hypohyal (Hhl, Figs. 20, 21, 25) is large and square, the upper (Hhu, Fig. 25) small and containing a passage for the hyoidean artery. In front of the hypohyals one specimen shows a small endochondral ossification (Bh, Fig. 20), presumably a basihyal, but no other specimen shows a basihyal. There was no basihyal tooth plate. There is a long, slender urohyal (Uh, Figs. 20, 25) differing from that of *Gaudryella* in having shorter ventro-lateral laminae which are not concave anteriorly.

There are seven (normally) or eight branchiostegals (Figs. 20, 21, 32), the first two (or three where eight are present) slender and rod-like, the remainder curved and spathiform, their breadth increasing from front to rear, with 'clupeoid projections' (McAllister 1968, fig. 1) at the bases of the last two. The last ray is extremely broad

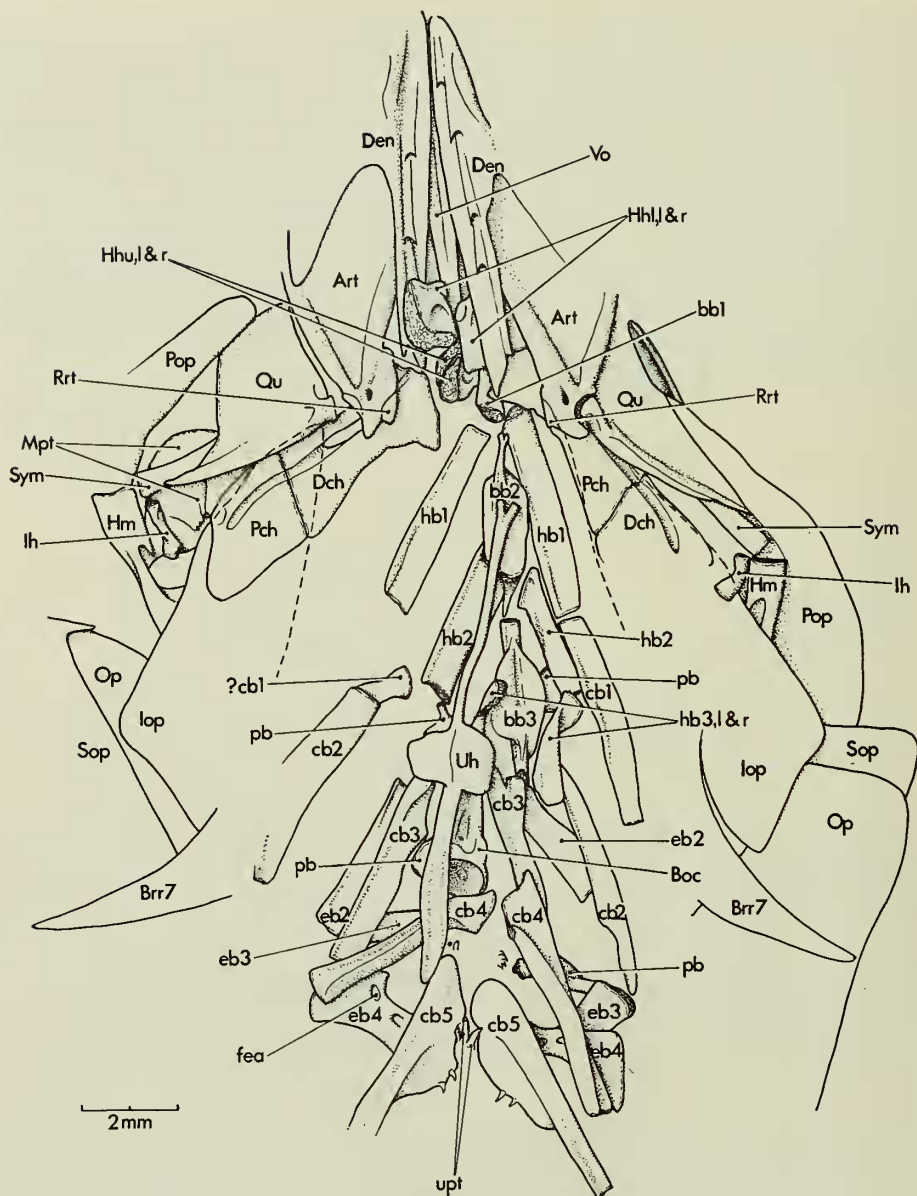


FIG. 25. *Humbertia operta* gen. & sp. nov. Dorso-ventrally crushed skull in ventral view showing the branchial skeleton. Simplified drawing of AM 4115, Hajula, Lebanon (cf. Pl. 5, fig. 1), branchiostegals omitted and anterior parts of left and right interoperculars drawn in transparency to show the ceratohyals. *bb* 1-3, basibranchials; *cb* 1-5, ceratobranchials; *eb* 2-4, epibranchials; *fea*, efferent arterial foramen in fourth epibranchial; *hb* 1-3, hypobranchials; *pb*, pharyngobranchials; *upt*, upper pharyngeal teeth; explanation of other abbreviations p. 296.

and crescentic. The last two branchiostegals articulate with the outer face of the proximal ceratohyal, the next articulates on the suture between the proximal and distal ceratohyals, and the first four or five on the distal ceratohyal.

(viii) *Branchial arches*. One specimen, AM 4115 (Pl. 5, fig. 1; Fig. 25), shows much of the gill-arch skeleton in ventral view. Though the bones are badly crushed and displaced, it is possible to recognise most of the elements. There are three ossified basibranchials (bb 1-3), the first short and broad, the second and third long and slender but each bearing a broad dermal plate, apparently toothless, fused with the endochondral ossification. There are three pairs of hypobranchials (hb 1-3) the first and second long, the third shorter and twisted, with antero-ventral processes which probably formed a partial canal for the ventral aorta. The third hypobranchials, though shorter than the second, are longer than in most living teleosts, where they are usually small bones. The five ceratobranchials (cb 1-5) are long, as usual, and the fifth is fused with an oval tooth plate bearing rather large, conical teeth. The dorsal parts of the gill arches are mostly unrecognisable, but the deep, axe-head shaped fourth epibranchial (eb 4), apparently perforated by an efferent arterial foramen (fea), is conspicuous, and the second and third epibranchials (eb 2-3) can be tentatively identified. The upper pharyngeals bear large, conical teeth (upt), like the lower, but the details of their supporting bones cannot be seen, nor are the anterior pharyngobranchials (pb) certainly identifiable. The gill arches bear toothless, leaf-like gill-rakers, reaching about 1.5 mm. in length in a fish of 24 mm. head length, considerably smaller than in *Gaudryella*.

(ix) *Opercular bones*. The preopercular (Pop, Figs. 19-21, 25) is similar to that of *Gaudryella* in shape except that the vertical limb is proportionally longer. The vertical limb extends up to the pterotic and there was no suprapreopercular. As in *Gaudryella*, the preopercular sensory canal ran in a closed tube close to the anterior edge of the bone, but the branches at and below the angle are longer and more complex. There are three main branches of the canal at the angle, the uppermost short and bifurcated once, the next bifurcated twice and extending to the edge of the bone, the lowermost bifurcating three times and also extending to the edge of the bone (Fig. 20). Anterior to this there is one short, simple branch, and the anterior part of the canal ran in a groove which is open ventrally, as in *Gaudryella*.

The opercular (Op, Figs. 19-21, 25) and subopercular (Sop, Figs. 19, 20, 25) differ from those of *Gaudryella* chiefly in the much greater relative size of the subopercular: the suture between the opercular and subopercular lies at about 45° to the anterior edge of the opercular compared with about 65° in *Gaudryella*, and the area of the subopercular is about equal to that of the opercular. There is no ornament and no squamation on the operculum. The interopercular (Iop, Figs. 20, 21, 25) is very long, as in *Gaudryella*.

(x) *Vertebral column*. There are 36-39 vertebrae (normally 38) and a free second ural centrum (Fig. 33). Fourteen to seventeen vertebrae are caudal (normally 15), 22-24 abdominal (normally 23). The centra are perhaps more heavily ossified than in *Gaudryella*, with stronger ridges on the surface (cf. Figs. 13-14, 26-27), but are perforated by a notochordal canal. On the first 18-20 vertebrae the neural arches and parapophyses are autogenous (Fig. 18). All but the last two or three of these

autogenous neural arches are paired structures, the neural spines being paired also. As in *Gaudryella* there are about seven supraneurals above the anterior vertebrae. The epineurals are outgrowths of the neural arch on the first 12-15 vertebrae. On more posterior vertebrae the epineurals are free, their point of attachment rising on to the neural spine. The epineurals are rod-like, as in *Gaudryella*, but extend a little further back, usually to about the third caudal vertebra. As in *Gaudryella* there are no ribs on the first two vertebrae; the ribs and parapophyses on the remaining abdominal vertebrae are similar to those of *Gaudryella* except that the parapophyses only increase in length on the last four vertebrae. There are rod-like epipleurals on the abdominal and first three or four caudal vertebrae. As in *Gaudryella*, the neural and haemal spines of pre-ural vertebrae 3-7 increase progressively in length and thickness, and the second pre-ural centrum has a low, broad neural spine. The caudal skeleton is described below, together with the caudal fin.

(xi) *Pectoral girdle and fin.* As in *Gaudryella*, the supratemporal (Stt, Figs. 15, 19) is a flimsy, scale-like bone, always more or less crushed into the post-temporal fossa. The bone is larger than that of *Gaudryella*, with its medial limb extending about half-way across the parietal. The sensory canal tube in the bone is triradiate, as usual, with a short antero-lateral limb, transmitting the temporal canal to the pterotic, and longer posterior and medial limbs. The medial branch of the canal, the supra-temporal commissure, has two or three posteriorly directed branches, and leads into the transverse groove on the parietal.

The post-temporal (Ptt, Figs. 15, 19) resembles that of *Gaudryella* in shape, with the curved dorsal limb almost meeting its fellow above the supraoccipital, but the sensory canal gave off three to five dorsal branches in the bone, compared with two in *Gaudryella*. The supracleithrum (Scl, Fig. 19) is more slender than that of *Gaudryella* but otherwise similar, and the cleithrum (Cl, Fig. 19) shows nothing to distinguish it from that of *Gaudryella*. There are two postcleithra, the upper rectangular and plate-like, the lower rod-like with an expanded head, extending postero-ventrally from the upper.

The endoskeletal pectoral girdle is partially visible in two specimens, but is poorly preserved and damaged in both. As in *Gaudryella* it consists of three ossifications, scapula, coracoid and mesocoracoid. The scapular foramen lies entirely within the scapula, and there is the usual large facet on the bone for the foremost fin-ray. The coracoid has a broad anterior process, and as far as it is visible seems to be like that of *Gaudryella*. The mesocoracoid is a narrow, arched strut on the inner face of the scapula and coracoid.

There are four proximal pectoral radials, similar in shape to those of *Gaudryella*. There is a series of distal pectoral radials, small nodular ossifications, apparently paired, lying between the bases of the fin-rays. There is a pair of distal radials between the hemitrichs of the first fin-ray, and at least three more pairs posteriorly.

The pectoral fin contains sixteen or seventeen rays, all segmented distally. The longest rays of the fin are equal in length to about seven vertebrae. As in *Gaudryella*, the upper hemitrich of the first ray is modified into a flat, scale-like structure, segmented distally. The base of this first upper hemitrich is also modified, being enlarged and perforated by a narrow canal.

(xii) *Pelvic girdle and fin.* The pelvic fins are inserted below the posterior part of the dorsal, at the level of the sixteenth or seventeenth vertebra. The pelvic girdle occupies a length of about four vertebrae, and appears to be identical with that of *Gaudryella*, except that the pelvic splint is separate, not fused with the girdle. There is no convincing evidence of ossified pelvic radials.

The pelvic fin contains a short, asymmetrical splint and twelve rays (four specimens and one fin of a fifth) or thirteen (one specimen and one fin of a second). All are segmented distally and the longest are equal in length to between five and six vertebrae, a little shorter than the pectoral rays.

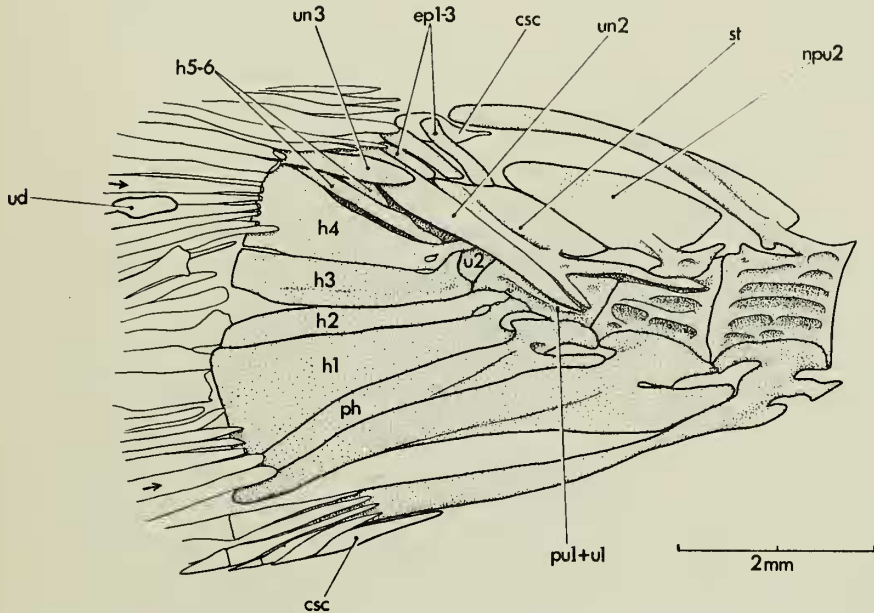


FIG. 26. *Humbertia operta* gen. & sp. nov. Caudal skeleton, slightly restored from P.48219 (holotype), Hakel, Lebanon. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

(xiii) *Dorsal and anal fins.* The dorsal fin (Fig. 33) originates over the eleventh vertebra and occupies a length of about six vertebrae, lying just in front of the mid-point of the back. The fin contains fourteen rays supported by thirteen radials. The first two radials are crowded together and the first has a stout anterior process from its head. The shaft of the first radial ends above the ninth vertebra. Except for the first four, the radials have separate ossified middle segments. The first fin-ray is short and unsegmented, though paired. The remaining rays are all segmented distally, and all but the second and third are branched. The longest ray, the fourth, is equal in length to seven vertebrae, and about equal to the maximum depth of the trunk.

The anal fin (Fig. 33) is small and remote, as in *Gaudryella*, originating below the

ninth or tenth pre-ural vertebra and occupying a length of three vertebrae. The fin contains eight short, segmented rays supported by seven radials. The shaft of the first anal radial lies behind the haemal spine of the fourth caudal vertebra.

(xiv) *Caudal skeleton and fin.* The caudal skeleton (Figs. 26, 27) is less specialised than that of *Gaudryella*. The neural spines of PU3-5 are long and slightly expanded distally, and have laminar anterior expansions near their bases, growing larger from front to rear. These neural arches are not autogenous. The haemal spines of PU2-5 are similarly expanded distally, and there are anterior laminar expansions on those of PU2 and PU3. The haemal arches of PU2 and PU3 are always autogenous, that of PU4 is sometimes so. The foremost procurent rays of the fin normally articulate with the neural spine of PU3 above and the haemal spine of PU3 or PU4 below, while the caudal scutes (csc, Fig. 27) extend forward to the neural spine of PU4 and the haemal spine of PU4 or PU5. PU2 has a low, leaf-like neural spine (npu2), as in *Gaudryella*, which is autogenous. The haemal spine of PU2 has a large anterior expansion and a smaller posterior one which fits closely against the anterior expansion of the parhypural, as in *Gaudryella*. The first pre-ural and ural centra are fused (pu1+u1), but in contrast to *Gaudryella* neither the parhypural, the lower hypurals nor the stegural is fused with this compound centrum. The parhypural (ph) has a hypurapophysis and an anterior expansion, paired at the base, articulating with the preceding haemal spine. The first hypural (h1) is very broad and articulates with the supporting centrum in the normal way. The slender second hypural (h2) is partially or completely fused with the first in about half the specimens, although in the remainder it is separate. This variation in the second hypural does not appear to be correlated with the size of the individual.

Articulating with the dorso-lateral surface of PU1 + U1 there is a large, autogenous stegural (st). The stegural consists of a shaft, forked proximally, and a dorso-medial expansion which extends forwards to fit against the neural spine of PU2, with a deep notch between it and the anterior part of the shaft of the bone. The upper fork of the stegural extends forwards across the dorso-lateral surface of PU2 and the short lower fork is applied to PU1 + U1, exactly as in *Elops* (Monod 1968, figs. 20-24) and *Nematonotus* (Patterson 1968b, fig. 25). The dorso-medial expansion of the stegural, representing the neural arches of PU1 and U1, seems to be very like that of *Gaudryella* (Fig. 13B), but it is not possible to tell whether the two stegurals are fused in the mid-line dorsally, as they are in *Gaudryella*. The second uroneural (un2) is similar to that of *Gaudryella* in length and position, but is broader. In contrast to *Gaudryella* there is a short third uroneural (un3) lying horizontally across the upper part of the second.

There is a small second ural centrum (u2), supporting four upper hypurals (h3-6). The third hypural is a little broader than the second, the fourth is almost as broad as the first, and the fifth and sixth are slender. As in *Gaudryella*, the head of the fifth hypural and the upper part of the head of the fourth extend forwards in slender points, dorso-lateral to the second ural centrum. There are three epurals (ep1-3), approximately equal in size.

The caudal fin is strongly forked and contains nineteen principal rays with seventeen branched. There are five to eight procurent rays above and below, the first

two or three small, leaf-like and unsegmented. A rather large caudal scute (csc, Fig. 27) is present in front of both the upper and lower procurent rays. As in *Gaudryella*, there is a single urodermal (ud) lying on the second ray below the uppermost principal ray.

(xv) *Squamation*. The scales are more clearly visible than those of *Gaudryella* and must have been thicker. As in *Gaudryella* they are acellular, large and cycloid, with continuous, well separated circuli. There appear to be eight scales in a transverse series on the trunk. There is a broad, continuous lateral line and as in *Gaudryella* the number of lateral line scales is approximately equal to the number of vertebrae. There are no scales on the cheek or operculum, and none on the bases of the fins.

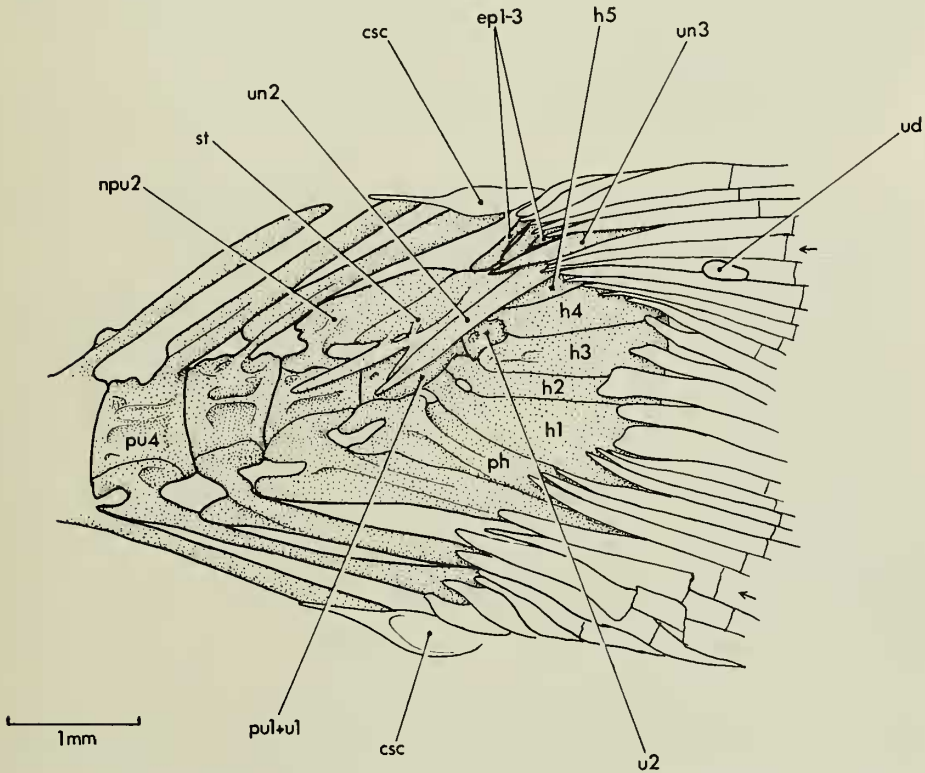


FIG. 27. *Humbertia aperta* gen. & sp. nov. Caudal skeleton as preserved in AM 5564, Hajula, Lebanon. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

(xvi) *Soft anatomy*. Muscle and retinal pigment are often preserved in the same manner as in *Gaudryella*, and fossilised gut contents (e.g. Pl. 4, fig. 2) show that the anus lay close in front of the anal fin. As in *Gaudryella* there is no evidence of an adipose fin. Chromatophores are sometimes preserved in specimens from Hajula as

pale spots under the scales : they indicate that the whole of the back was densely pigmented while the belly was light. The scales consist of acellular bone, but, as in *Gaudryella*, although most of the skeleton is also acellular, certain areas, mostly close to articular surfaces, contain many chondrocyte-like spaces. These areas include the head of the vomer, palatine and maxilla, the edge of the diastema on the dentary and the glenoid area of the endoskeletal pectoral girdle.

IV. DISCUSSION

(a) Similarities between *Gaudryella* and *Humbertia* and evidence of euteleostean relationships.

In addition to general similarities in size, body form, fin size and disposition, geological occurrence, etc., *Gaudryella gaudryi* and *Humbertia aperta* share the following anatomical features :—

1. Supraoccipital small and parietals in contact medially
2. Post-temporal fossa roofed
3. Well developed bone-enclosed parietal and epiphyseal branches of supraorbital canal on frontal
4. Nasals slender and laterally placed
5. Large supraorbital and small, comma-shaped antorbital present
6. Trigemino-facialis chamber with three major external openings
7. Orbitosphenoid and basisphenoid well developed
8. Lachrymal large, second infraorbital slender, posterior infraorbitals extend to preopercular
9. Dermosphenotic large and triangular, the infraorbital sensory canal ending blindly anteriorly
10. Premaxilla small, maxilla with small, clustered teeth and bearing two mobile supramaxillae
11. Palatine without a maxillary process, with a ball and socket joint with the maxilla
12. Hyomandibular broad and vertical
13. Distal ceratohyal perforated by a fenestra
14. No scales on cheek or operculum
15. Anterior neural arches and parapophyses autogenous, anterior epineurals fused with neural arches
16. Seven or eight supraneurals above anterior vertebrae
17. Post-temporals almost in contact medially, attached to epiotics by ligaments
18. Mesocoracoid present, coracoid deep
19. Four proximal pectoral radials, several small distal radials
20. Pectoral fin low on flank, with about 16 rays, upper hemitrich of first ray laminar
21. Pelvis abdominal, with a splint and 12-13 rays
22. Anal fin small and remote
23. Scales large and cycloid, lateral line complete
24. Neural spine of second pre-ural centrum short and broad
25. Free second ural centrum present

26. First uroneural forked proximally
27. Caudal fin forked, with nineteen principal rays
28. Upper and lower caudal scutes and one urodermal present
29. Supratemporal a flimsy bone overlying post-temporal fossa, supratemporal commissure passes medially in a groove on the parietal
30. Vomer with a very long posterior process
31. Occipital condyle formed by basioccipital only
32. Intercalar small
33. Antorbital not penetrated or grooved by the infraorbital sensory canal
34. Symplectic and quadrate inclined forwards, mandibular articulation below centre of orbit.
35. Ectopterygoid and endopterygoid toothless
36. Dentary with a long, high coronoid process, with a deep pocket for the lip ligaments on its outer face
37. Urohyal very long and slender, with a broad, horizontal ventral flange
38. Toothless gill-rakers on gill arches
39. No ribs on first two vertebrae
40. Rod-like epipleurals on abdominal vertebrae
41. Two postcleithra, the upper scale-like, the lower rod-like
42. Anteriorly directed flanges on last two neural spines and last three haemal spines
43. First pre-ural and ural centra fused
44. Six hypurals, fifth and sixth with paired anterior processes alongside second ural centrum
45. First uroneural fused with neural arches of first ural and pre-ural centra to produce a stegural
46. Scales and most of skeleton acellular.

Of the characters in this list, numbers 1-28 are all probably primitive for teleosts (cf. leptolepids and pholidophorids, Rayner 1937 ; Nybelin 1962, 1966 ; Patterson 1967b, 1968a ; Wenz 1968 ; etc. : for the infraorbitals see Nelson 1969b ; for the maxillo-palatine joint see Schaeffer & Rosen 1961, Vrba 1968 ; for the ceratohyal see Rosen & Patterson 1969 : 408 ; for the second pre-ural neural spine see Patterson 1968b ; for the first uroneural Patterson 1968a). These primitive characters demonstrate that the two genera are teleosts of very primitive grade, but they are without much value in indicating relationships. Characters 29-46 are all probably advanced in some degree over the basic teleostean condition. The most significant of these advanced characters seem to be those of the caudal skeleton, numbers 42, 43 and 45. These three features, fusion of the first pre-ural and ural centra, the development of a stegural, and flanges on the last few neural and haemal spines (Gosline 1960 : 332) are each known to occur only in members of the Euteleostei (Greenwood *et al.* 1967). That this is the correct position of the two genera is also indicated by other advanced features such as the form of the supratemporal and supratemporal commissure (which passes through or over the supraoccipital in clupeomorphs, behind the parietal in elopiforms), the small intercalar (large and with an anterior strut across the sub-temporal fossa in primitive osteoglossomorphs and elopomorphs), the absence of a

sensory canal in the antorbital (bone enclosed and with neuromasts in osteoglossomorphs and elopiforms : Nelson 1969b), the rod-like epipleurals (absent in osteoglossomorphs, usually forked in clupeomorphs), and the acellular bone of the skeleton (cellular in osteoglossomorphs, in elopiforms and eels amongst elopomorphs, and in almost all clupeomorphs : Kölliker 1859, Moss 1961).

Relationships with the euteleosteans are not opposed by any of the primitive characters common to *Gaudryella* and *Humbertia*, or by those known in only one of the two genera (such as the rudimentary basipterygoid process in *Humbertia* and the separate rostral of *Gaudryella*), for all are known to occur amongst generalised euteleosteans in a mosaic distribution (a basipterygoid process is reported in the alepocephaloid *Searsia* by Gosline (1969 : 196) ; a perforate ceratohyal has not yet been recorded in primitive euteleosteans (see McAllister 1968) but is often present in *Coregonus* (Fig. 28)). Unfortunately, we do not know whether either fossil genus had an adipose fin, the chief distinguishing feature of generalised euteleosteans.

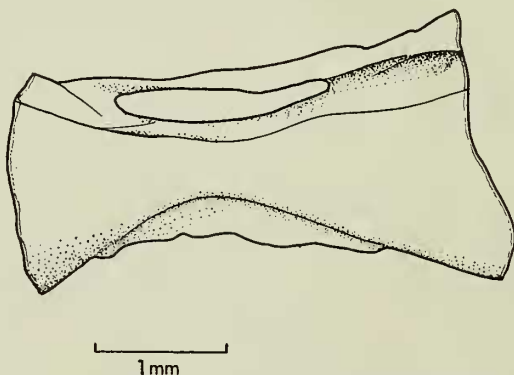


FIG. 28. *Coregonus lavaretus* L. Left distal ceratohyal of a 70 mm. individual in lateral view to show the fenestra. Recent, R. Gotha, Sweden, 1853.3.16.18.

(b) Differences between *Gaudryella* and *Humbertia* and relationships within the Euteleostei.

Amongst the Euteleostei, the area in which relatives of *Gaudryella* and *Humbertia* are to be found can be restricted to those groups in which the first ural and pre-ural centra are fused, i.e. the salmoniform suborders Argentinoidei, Galaxioidei, Osmeroidi and Stomiatoidei (the last two closely related according to Weitzman 1967b, but see Nelson 1970), the superorder Ostariophysi (including the gonorynchiforms, Rosen & Greenwood 1970), and the superorder Neoteleostei (ctenothrissiforms + myctophiforms + paracanthopterygians + acanthopterygians, Rosen & Patterson 1969 ; Nelson 1969a : 534).

The ostariophysans can be excluded from consideration for the following reasons :

1. There is no sign in *Gaudryella* and *Humbertia* of the anterior vertebral specialisations which characterise even the most primitive of these fishes (Rosen & Greenwood 1970 ; for the caudal skeleton see below, p. 276).

2. Ostariophysans are represented in the same beds as *Gaudryella* and *Humbertia*

by the gonorynchid *Charitosomus hakelensis*. This fish shows the typical jaws, pharyngeal teeth, caudal skeleton (Fig. 45), etc., of the gonorynchids, indicating that the gonorynchiforms (and therefore also the ostariophysans) were fully differentiated at that time.

3. The skeleton still consists of cellular bone in most members of both ostariophysan orders, and in the gonorynchiform *Chanos* (Kölliker 1959, Moss 1961 : *Charitosomus* appears to be acellular). *Gaudryella* and *Humbertia*, which are almost entirely acellular, are more advanced and can hardly be primitive members of this group.

The neoteleosts will also be left out of consideration, for reasons which are perhaps less convincing than those excluding the ostariophysans. In the same beds as *Gaudryella* and *Humbertia*, the neoteleosts are abundantly represented by myctophiforms (*Nematonotus* [Aulopidae], *Sardinioides* and *Cassandra* [? Neoscopelidae], *Acrognathus*), ctenothrissiforms (*Ctenothrissa*, *Pattersonichthys* [Goody 1969]) and acanthopterygians (*Hoplopteryx*, *Lissoberyx* [Trachichthyidae], *Stichocentrus*, *Caprobberyx* [Holocentridae], *Aipichthys*, *Pycnosteroideus*). These fishes are easily recognisable, principally by the advanced position of the pelvis, the pectorals high on the flank, and the absence of a mesocoracoid. Lack of these specialisations in *Gaudryella* and *Humbertia* does not necessarily exclude these fishes from the Neoteleostei, but does mean that they could only be extremely primitive members of the group, especially in view of the structure of their jaws, palatine and ethmoid. In such a position it is improbable that the dentition would be as reduced as it is in *Gaudryella* and *Humbertia*, for primitive members of all major neoteleostean lineages are notably well toothed on the jaws, palate, gill arches and gill-rakers, and also have a larger gape than *Gaudryella* and *Humbertia*. There are no advanced characters which definitely exclude *Gaudryella* or *Humbertia* from relationship with the neoteleosts, but they are certainly of more primitive grade than the latter. And whilst reduction of the gape and dentition in *Gaudryella* and *Humbertia* make such a relationship improbable, the absence in both of any of the advanced characters of the neoteleosts make further discussion of the possibility futile.

The remaining groups, the argentinoids, galaxioids, osmeroids and stomiatoidei, are the only likely relatives of *Gaudryella* and *Humbertia*, and the two genera must be placed with them in the order Salmoniformes. None of these groups is reliably recorded in the Cretaceous. Osmeroids are first known in the Pleistocene, galaxioids in the Pliocene and argentinoids in the Oligocene. Various Cretaceous fishes have been placed in the Stomiatoidei, but these are critically discussed by Weitzman (1967b).

In considering these four salmoniform suborders, one is immediately struck by the many characters common to the two fossil genera and the argentinoids, especially *Argentina*. These include the body form, the size, composition and position of the fins (cf. illustrations in Cohen 1964), the large scales, reduced dentition, small jaws, short gape, long lower limb of the preopercular, long posterior process of the vomer, expanded posterior infraorbitals, structure of the skull roof, with the parietals in contact, the post-temporal fossa roofed and similar frontals (cf. Figs. 3A, 29A ; and illustrations in Chapman 1942a, b, 1943, 1948), and the vertebrae, where the epineurals

are fused with the autogenous neural arches anteriorly, the parapophyses are autogenous, and epipleurals are present (at least in *Argentina*). However, in argentinoids there are marginal vomerine teeth (central and longitudinal in *Gaudryella*, absent in *Humbertia*), the basihyal (Nelson 1970) is long and primitively toothed (short in *Gaudryella*, toothless in *Humbertia*), the premaxilla and maxilla are toothless, and there are no supramaxillae. Also, in *Argentina*, one of the most primitive genera, the skeleton is cellular (Kölliker 1959 ; personal observations), and even in *Bathylagus*, which is advanced in having the parietals separate, no mesocoracoid, no swim-

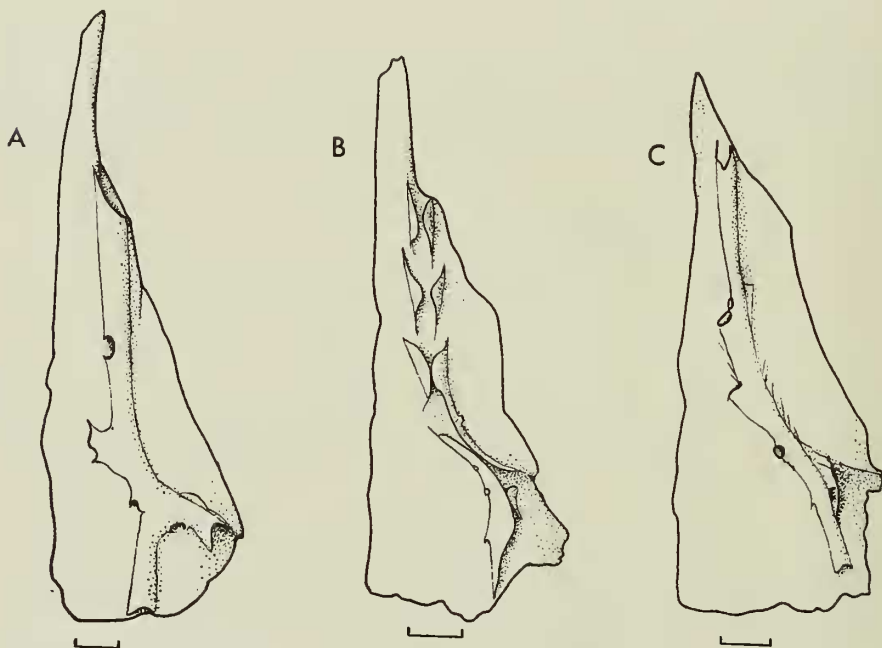


FIG. 29. Right frontals in dorsal view of A, *Argentina sialis* Gilbert, Recent, N.E. Pacific, 1967.3.5.2, 72 mm. ; B, *Hypomesus olidus* (Pallas), Recent, Tartar Strait, 1925.8.6.9, 93 mm. ; C, *Coregonus lavaretus* L., same specimen as Fig. 28. Scale 1 mm.

bladder, etc., the skeleton is still cellular (personal observation). This suggests that all argentinoids retain cellular bone and are therefore more primitive than the almost acellular *Gaudryella* and *Humbertia*.

The osmeroids and stomiatooids are acellular, like *Gaudryella* and *Humbertia*, but are primitively well toothed forms, with endopterygoid, basihyal and basibranchial teeth. In this they are more primitive than *Gaudryella* and *Humbertia*, while they are more advanced in having slender posterior infraorbitals, the neural arches and parapophyses fused with the centra (except in *Plecoglossus*, Weitzman 1967b : 531), no orbitosphenoid, etc.

The galaxioids have recently been revised by McDowall (1969) and shown to comprise two groups, one containing the galaxiids and aplochitonids, the other the

TABLE 3

Differences between *Gaudryella gaudryi* and *Humbertia operta*

Character	<i>Gaudryella gaudryi</i>	<i>Humbertia operta</i>
1. Maximum standard length	90 mm	115 mm
2. Parietals	Almost square, groove for supratemporal commissure short and shallow	Shorter and broader, groove for supratemporal commissure longer and deeper
3. Nasals	Short, trough-like	Long, tubular
4. Ethmoid	Rostral and mesethmoid separate, triradiate anteriorly, rostral overlying frontals posteriorly	Rostral and mesethmoid fused, disc-like anteriorly, underlying frontals posteriorly
5. Vomer	Narrow, with a median row of teeth	Broader, toothless
6. Parasphenoid	Notched by efferent pseudobranchial artery, without basipterygoid process	Pierced by efferent pseudo-branchial artery, with rudimentary basipterygoid process
7. Posterior infraorbitals	One large bone	Two bones
8. Head of hyomandibular	Double	Single
9. Metapterygoid	Reduced	Normal
10. Palatine	Toothless	Toothed
11. Premaxilla	25% length of maxilla, toothless, without distinguishable ascending and articular processes	40% length of maxilla, toothed, with rudimentary ascending and articular processes
12. Symphyseal end of dentary	Serrated	Smooth
13. Oral margin of dentary	With a few small teeth near symphysis	Small teeth near symphysis, larger, blade-like teeth behind
14. Inner face of dentary	With large pocket for tip of angulo-articular	With minute pocket for Meckel's cartilage
15. Distal and proximal ceratohyals	Separated by cartilage	Sutured together on medial surface
16. Basihyal	Unossified, covered by toothplate	Small ossification, no tooth-plate
17. Branchiostegals	11, last two spathiform	7-8, last five spathiform, crescentic posteriorly
18. Branches of preopercular sensory canal	Short	Long, dichotomising
19. Subopercular	Upper edge at 25°, smaller than opercular	Upper edge at 45°, about as large as opercular
20. Vertebrae	mean 43, 28 + 15	mean 38, 23 + 15
21. Autogenous neural arches	12-15	18-20
22. Epineurals fused with neural arches	8-10	12-15
23. Branches of sensory canal in supra- and post-temporal	2 ; none	3-5 ; 2-3
24. Origin of pelvic fin	below vertebra 21	below vertebra 16
25. Pelvic splint	fused with girdle	autogenous
26. Origin of dorsal fin	over vertebra 15-16	over vertebra 11
27. Dorsal fin	12 rays, 12 radials, last radial with no fin-ray	14 rays, 13 radials

Table 3—continued

Character	<i>Gaudryella gaudryi</i>	<i>Humbertia aperta</i>
28. Anal fin	9 rays, 8 radials	8 rays, 7 radials
29. Lamellar expansions on last few neural and haemal spines	on NPU ₂ -3, HPU ₂	on NPU ₂ -5, HPU ₂ -3
30. Parhypural and lower hypurals	fused with centrum and each other	autogenous
31. Hypurals three and four	partially fused	separate
32. Stegural	fused with centrum	autogenous
33. Third uroneural	absent	present
34. Epurals	2	3
35. Caudal scutes	small	large
36. Scales	very thin	thicker

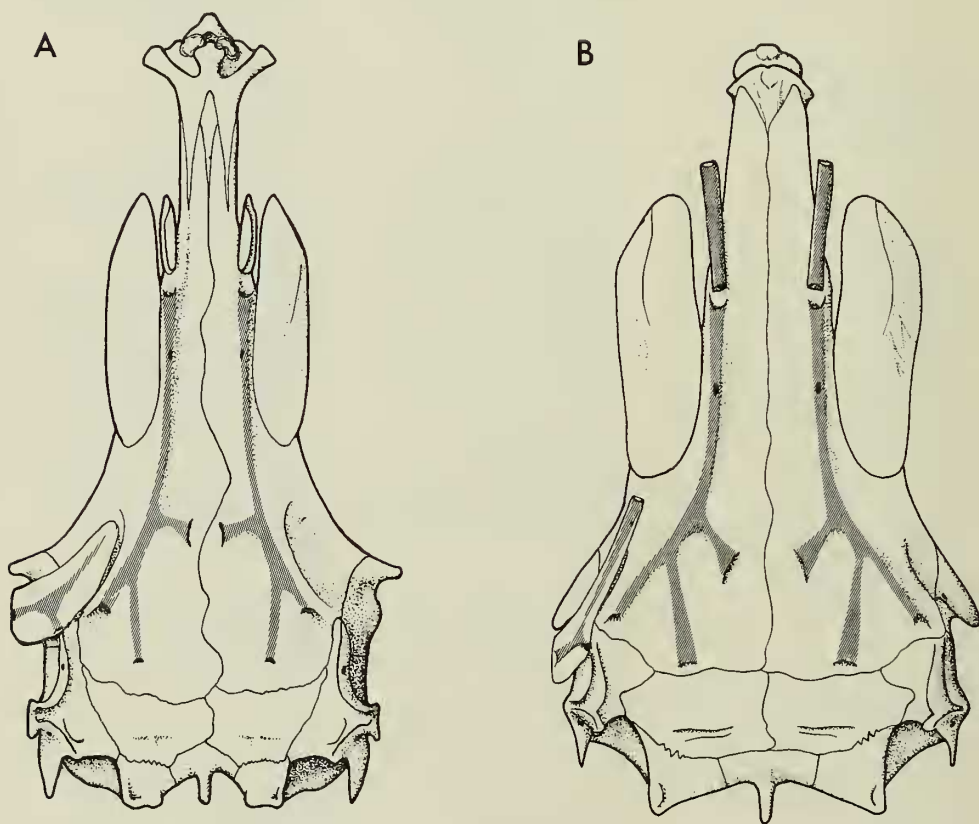


FIG. 30. Restorations of skull roof in dorsal view, A, *Gaudryella gaudryi* (Pictet & Humbert), B, *Humbertia aperta* gen. & sp. nov. Both $\times 6$ approx. Bone-enclosed sensory canals cross-hatched. Both Middle Cenomanian, Hakel and Hajula, Lebanon.

retropinnids and prototroctids. Galaxioids are acellular, but have a low, well toothed mandible and endopterygoid teeth. They are advanced over *Gaudryella* and *Humbertia* in many ways, notably in having the ectopterygoid reduced or absent, a

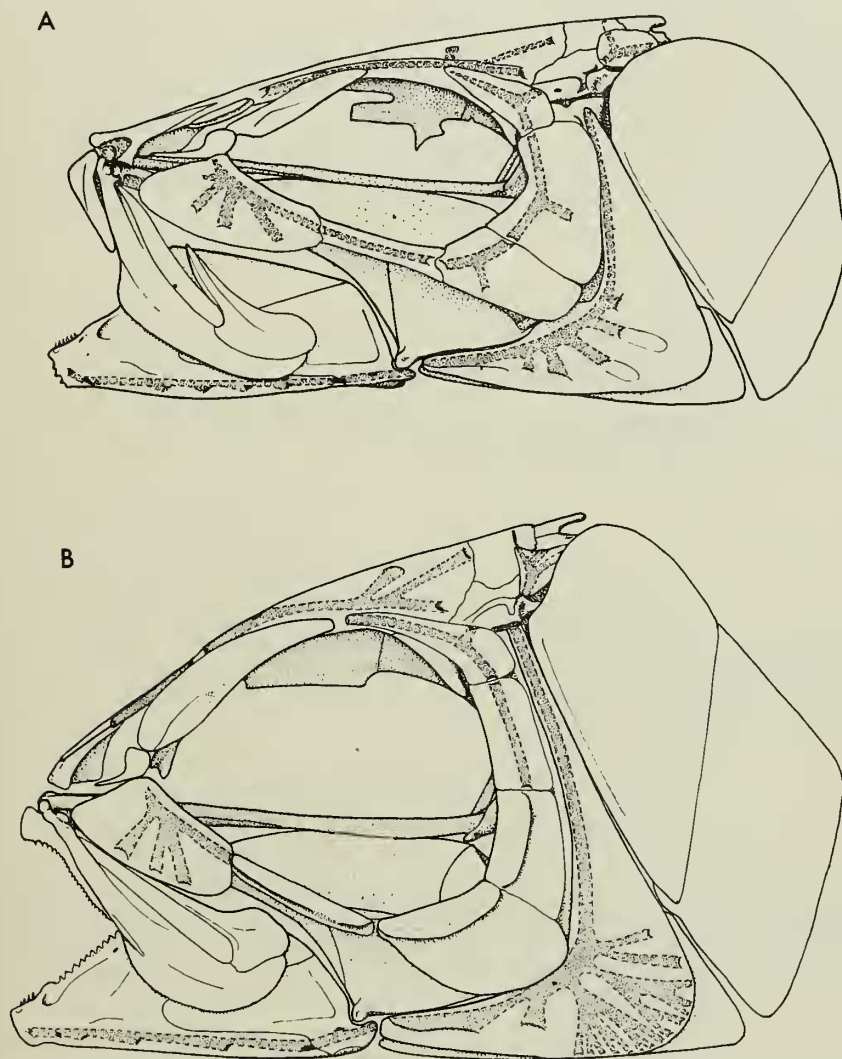


FIG. 31. Restorations of skull in lateral view, A, *Gaudryella gaudryi* (Pictet & Humbert), B, *Humbertia aperta* gen. & sp. nov. Both $\times 5$ approx., Middle Cenomanian, Hakel and Hajula, Lebanon.

narrow or incomplete infraorbital series, no supramaxillae, orbitosphenoid or mesocoracoid, the neural arches and parapophyses fused with the centra, and less than nineteen principal caudal rays.

Before discussing these and other resemblances, it is necessary to consider the differences between *Gaudryella* and *Humbertia*, which are listed in Table 3 and summarised in Figs. 30-33.

Many of these differences appear relatively trivial, such as are commonly found within a genus or family. Others are surely of greater significance, such as the structure of the ethmoid region (4), parasphenoid (6), infraorbitals (7), jaws and dentition (5, 10, 11, 12, 13, 16), hyoid and branchiostegals (15, 16, 17), operculum (19) and caudal skeleton (30-34). In the parasphenoid, infraorbitals, toothed palatine and premaxilla, large subopercular, several features of the caudal skeleton, and in various minor features such as those of the vertebrae and the more numerous, bone-enclosed branches of the sensory canals, *Humbertia* is the more primitive of the two

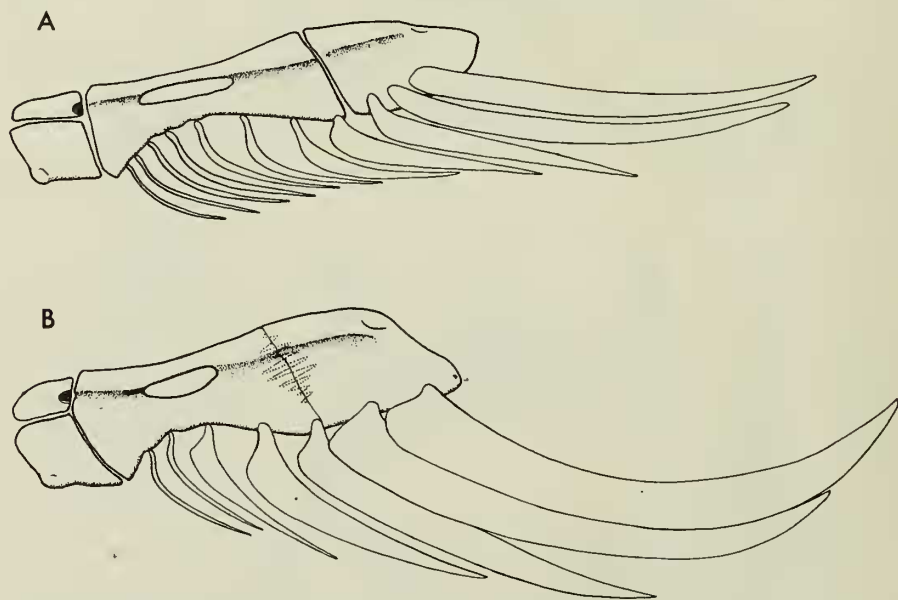


FIG. 32. Restorations of left hyoid bar and branchiostegals in lateral view, A, *Gaudryella gaudryi* (Pictet & Humbert), B, *Humbertia aperta* gen. & sp. nov. Both $\times 8$ approx., Middle Cenomanian, Hakel and Hajula, Lebanon. The dotted line across the ceratohyal in B indicates the splints of bone suturing the distal and proximal ceratohyals on the medial surface.

(for the subopercular cf. leptolepids and pholidophorids, Nybelin 1962, 1966), but in the ethmoid (see below), toothed vomer and basihyal, and in the hyoid and branchiostegals, *Gaudryella* is more primitive, showing that there can be no close relationship of ancestor-descendant type between the two. There is little that can be said about some of these differences, such as those concerning the specialisations of the posterior infraorbitals and pelvic spint in *Gaudryella*, since in both these features it is unique, so far as I know (for the infraorbitals, cf. Nelson 1969b). Other

major differences will be discussed in relation to the conditions in argentinoids, galaxioids, osmeroids and stomiatoids.

(i) *Ethmoid region*

Weitzman (1967b) has recently discussed the ethmoid ossifications of salmoniform fishes but in view of his conclusions further consideration of these bones is necessary, although the evidence on which my own opinions are mainly based, the structure of the ethmoid region in Jurassic pholidophorids and leptolepids, will be presented fully elsewhere. Weitzman concluded (pp. 524, 527) that the pattern of ethmoid bones found in the osmerid *Spirinchus* is primitive for salmoniforms. In *Spirinchus* there are seven laminar ethmoid bones : paired proethmoids and capsular ethmoids, and median supraethmoid, ventral ethmoid and anterior myodome bones. The proethmoids are superficial and presumably dermal, the remainder are perichondral ossifications of the ethmoid cartilage. There is no endochondral ossification. Weitzman finds this pattern to be primitive because it is complete in what he believes is the most primitive osmerid and is little modified in primitive stomiatoids, more so in advanced ones. Weitzman does not discuss the alternative view, that these numerous ethmoid bones are the result of fragmentation, writing only that such a hypothesis 'seems untenable' : I would maintain it, however. The opposing hypotheses of fusion and fragmentation in various parts of the fish skeleton have been widely discussed, with regard to the dermal bones (e.g., Devillers & Corsin 1968, Ørvig 1968) and the endoskeleton (e.g., Jarvik 1954, 1965, Nelson 1969a). In the snout of actinopterygians it is now well established that the overall trend throughout the evolution of the group has been towards fragmentation, not fusion, in both the dermal bones (Gardiner 1963) and the endoskeleton (Nielsen 1942, 1949). In discussing the details of the ethmoid ossifications in teleosts and their forerunners it is necessary first to distinguish between dermal bones and the endoskeleton, although this is often very difficult, even when careful embryological work has been done (e.g. in *Salmo*, see Pehrson 1944 : 146 ; de Beer 1937 : 126).

The *dermal skeleton* of the ethmoid region is primitively formed in teleosts by only one dorsal bone, the rostral, primitively separate from the underlying endoskeleton and enclosing the ethmoid commissure, which may be subsequently reduced to a pit-line. Whether the rostral of the teleost lineage was originally paired or unpaired is not yet known (see Griffith & Patterson 1963 : 34), and perhaps such a question has little meaning since in *Lepisosteus* (Hammarberg 1937 : 287) and *Amia* (Pehrson 1940 : 9) the rostral develops from paired rudiments which soon fuse to produce the median rostral characteristic of the adult fish. The paired origin of the rostral in ontogeny is due to the influence of the invaginated neuromasts of the ethmoid commissure, which are paired. Pehrson's study of the embryology of *Esox* (1944) shows that the paired proethmoids of this fish are undoubtedly homologous with the median, canal-bearing rostral of holosteans and primitive teleosts, since the proethmoids originate in relation to the organs of the ethmoid commissure, here reduced to a pit-line. Presumably, only when the influence of the sense organs declines further can the rostral originate as a median bone, as it does in *Salmo* (Pehrson 1944 : 145 ; Devillers 1948 : 39) and many higher teleosts. Further evidence of the homology of

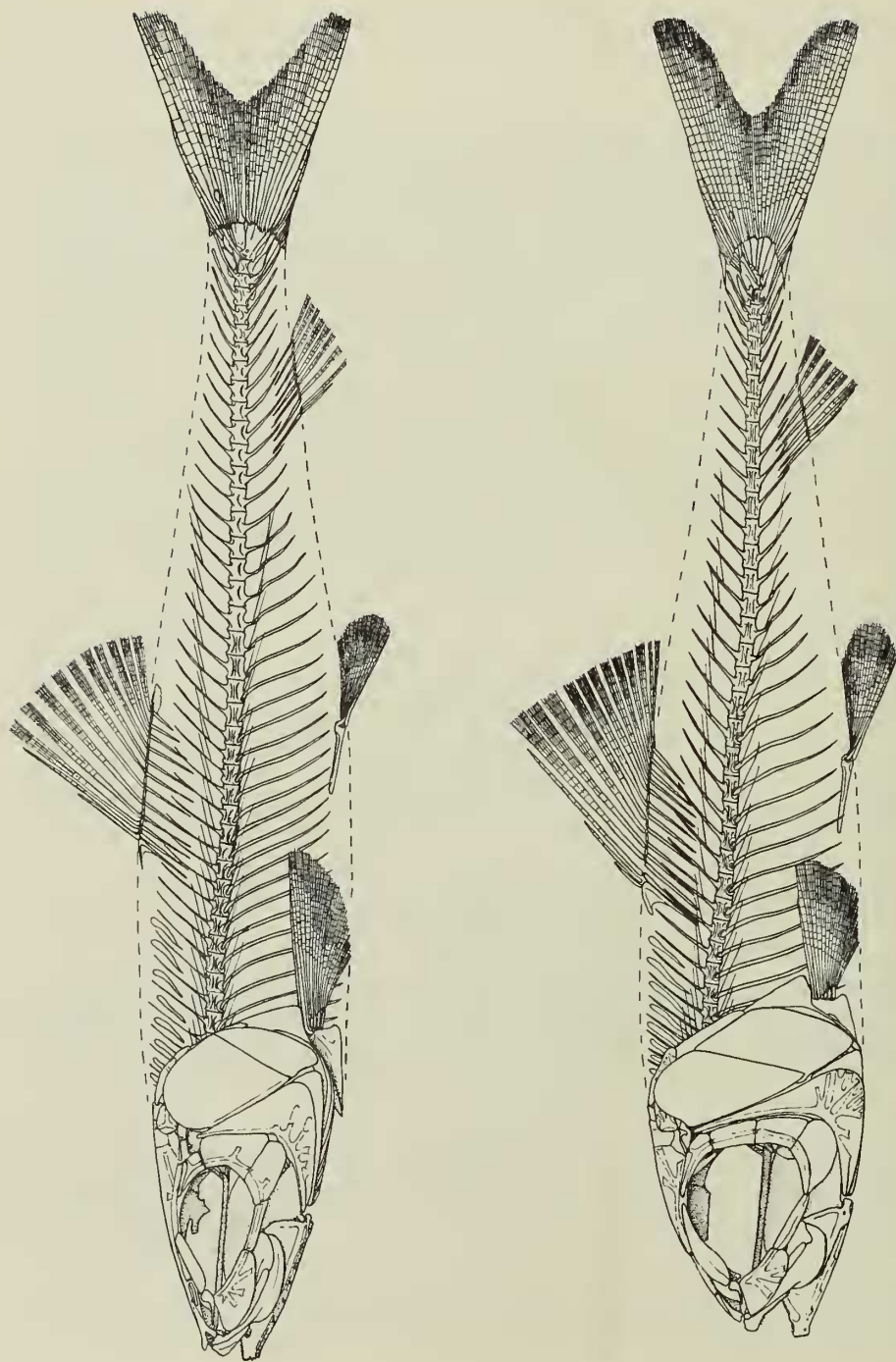


FIG. 33. Restorations of the skeleton, scales omitted, of *Gaudryella gaudryi* (Pictet & Humbert) (above) and *Humbertia aperta* gen. & sp. nov. (below). Both $\times 2\frac{1}{2}$ approx., Middle Cenomanian, Hakel and Hajula, Lebanon.

paired proethmoids and a median rostral is furnished by the identical morphological relationships of the proethmoids in osmerids such as *Spirinchus* and *Thaleichthys* compared with the median rostral of the osmerid *Hypomesus*.

In all the pholidophorids that I have examined the rostral is a broad, shield-like, unpaired bone, carrying a bone-enclosed ethmoid commissure whose width is about equal to the distance between the left and right posterior nostrils (see also Nybelin 1966 ; 1967a, fig. 1 A-C). In the Lower Jurassic *Leptolepis coryphaenoides* the rostral is already fused with the underlying endoskeletal ossifications (Rayner 1937 ; Wenz 1968 : 202 ; personal observations) and the ethmoid commissure is very short (Fig. 34). Wenz, with abundant material of *L. coryphaenoides*, finds that the ethmoid commissure may be bone-enclosed or a pit-line, and more significantly that the rostral, usually unpaired, is frequently divided by a median suture (1968, fig. 89). I have not observed this condition with certainty in *L. coryphaenoides* (ten ethmoids available), nor in the Upper Jurassic *L. sprattiformis*, where Wenz (1968 : 204) finds a paired

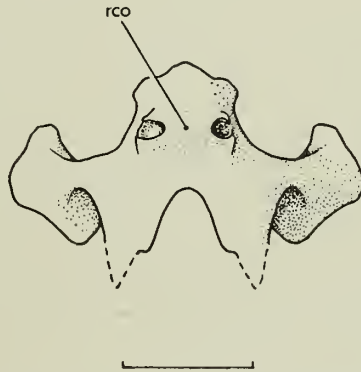


FIG. 34. *Leptolepis* sp. Isolated rostral in dorsal view, restoration based on P.51288, from stomach contents of a *Pholidophorus*, Oxfordian (Upper Jurassic), Dives, Normandy, France. Scale 1 mm. *rco*, rostral commissure.

rostral to be a constant feature, and indeed it is difficult to see how paired rostrals could exist when the rostral is already fused with the endoskeleton. But if Wenz is correct in these observations, *L. coryphaenoides* provides the earliest evidence of the existence of proethmoids, and that proethmoids and a median rostral should exist in the same species is further indication that there is no essential difference between the two conditions. Amongst living teleosts, all those with a bone-enclosed ethmoid commissure have a median rostral. Only in forms where the commissure has been reduced to a pit-line (or lost) do paired proethmoids appear (esocoids, some osmerids and stomiatoids).

In search of homologues of the proethmoids amongst other primitive teleosts, Weitzman (1967b : 526) refers to the ventro-lateral processes of the rostral in *Megalops* (Fig. 35A), which cap the cartilagenous anterior walls of the nasal capsules, and in large individuals meet an anterior process of the lateral ethmoid below the nasal capsule.

Weitzman suggests that fusion between these processes and the body of the rostral is incomplete in small specimens (36–75 mm.) and considers it possible that they are independent ossifications. Although these processes are absent in *Elops*, they are present in the Upper Jurassic *Anaethalion* (Nybelin 1967b, pl. 7, pl. 8, figs. 1, 2), which appears to be a close relative of the elopoids. Exactly similar ventro-lateral processes are also present in the Jurassic leptolepids (Wenz 1968, figs. 84, 89 ; Fig. 34). In *L. coryphaenoides* (Upper Lias) they are continuous with the rostral and partially fused with the underlying peri- and endochondral bone. But in a primitive, undescribed leptolepid from the Lower Lias this process is apparently separate from the rostral, extending towards the mid-line below it. The process is underlain by a distinct layer of perichondral bone and is therefore presumably dermal in origin. After removal of the rostral in this primitive leptolepid these processes are strikingly similar to the 'proethmoids' of the stomiatoid *Polymetme* (Weitzman 1967b, fig. 12). These lateral processes therefore appear to be distinct from the rostral in *Megalops* and in early leptolepids. They can hardly be considered part of the rostral since in *Megalops* they are overlain by a separate, canal-bearing lateral rostral (Nybelin 1967a, fig. 2B, C). Berg (1955, figs. 190, 191) found a pair of small, presumably dermal bones ('parethmoid') lying lateral to the rostral in *Coregonus lavaretus*. I have not found these bones myself, nor were they present in any of the eight North American species of *Coregonus* investigated by Norden (1961), but they might be relevant to the lateral processes of the rostral. The problem of the origin of this apparently dermal lateral process is analogous to the question of the existence of a dermal 'pre-frontal', which some investigators have found as a separate element in embryos of *Amia* and various teleosts, later fusing with the perichondral lateral ethmoid. As in the case of the lateral process of the rostral, there is no dermal bone in more primitive actinopterygians with which a prefrontal can be satisfactorily homologised.

While it is obvious that there are many unsolved problems in the dermal bones of the ethmoid region of teleosts, some conclusions can be listed by way of summary :

1. The unpaired, canal-bearing rostral of pholidophoroids, leptolepids and elopoids is homologous with the unpaired dermal bone below the ethmoid pit-line in salmonids, some osmerids, etc. ; with the superficial part of the compound mesethmoid of many higher teleosts ; and with the paired proethmoids of esocoids, some osmerids and stomiatoids.

2. The rostral is primitively separate from the underlying peri- and endochondral ossifications, and fusion between the two is an advanced feature.

3. No decision is possible on whether the rostral is primitively paired (proethmoids) or median (rostral), but in those teleosts where proethmoids are present (esocoids, osmerids, stomiatoids) they appear to be a neotenous character associated with the persistent influence of the sense organs of the ethmoid commissure.

4. The lateral processes of the rostral in *Megalops* and leptolepids may primitively have been independent ossifications whose origin is unknown.

The *endoskeleton* of the ethmoid region in palaeoniscoids and various 'subholosteans' is part of a single, massive ossification, extending back to the occipital fissure (Nielsen 1942, 1949 ; Rayner 1948, 1951 ; Lehman 1952). In the Lower Triassic parasemionotids, sutures appear separating a preorbital ossification from

an orbito-temporal (Lehman 1952, fig. 105), and a similar single preorbital ossification is found in the Jurassic 'holosteans' *Caturus*, *Aspidorhynchus* (Rayner 1948) and *Heterolepidotus* (personal observation). In the Upper Jurassic pholidophoroid *Ichthyokentema* the preorbital region is also occupied by a single large ossification (Griffith & Patterson 1963), but in pholidophorids there are usually three ossifications, paired lateral ethmoids and a mesethmoid, as in leptolepids and most living teleosts.

In many primitive living teleosts the endoskeleton of the ethmoid region is very poorly ossified (elopiforms, salmonines, *Chanos*, osmerids, etc.) ; a heavily ossified ethmoid is more common in higher groups such as the ostariophysans, myctophiforms and acanthopterygians. This has led Starks (1926), Weitzman (1967b) and others to the conclusion that a lightly or superficially ossified ethmoid is the primitive condition in teleosts, a reversal of the trend exemplified by the fossil evidence summarised above. Weitzman surmises that endochondral bone was re-introduced and that separate perichondral bones fused in several groups as adaptations to increased mobility or power of the jaws. But on this hypothesis one would predict that such fishes as the leptolepids, small, primitive and almost edentulous teleosts which were certainly microphagous, should have a very lightly ossified ethmoid region. In fact this is not so : in the more primitive leptolepids the mesethmoid is a solid mass of endochondral bone. A heavily ossified mesethmoid is also the rule in Cretaceous teleosts, irrespective of the form of the jaws (Patterson 1964, Goody 1969). In the endoskeleton of the gill arches, Nelson (1969a : 521) concludes that 'there is no known example of simple fusion between separate bones or ossification centres', and one might expect the same to be true of the neurocranium.

The alternative hypothesis, advocated here, is that a heavily ossified mesethmoid is primitive for teleosts, in agreement with the general trend in actinopterygians (and other fishes) and with the evidence of fossil teleosts. One would then assume that in certain groups such as osmerids and stomiatoids the reduction in ossification of the ethmoid has proceeded further in the more primitive members, perhaps because they have more lightly toothed or less mobile jaws. The several ethmoid ossifications of primitive osmerids and stomiatoids would thus be an advanced feature providing evidence that the two groups are related, which they would not do if Weitzman's assumptions were correct.

Weitzman predicted (1967b : 527) that the five perichondral ethmoid bones of some osmerids and stomiatoids (supraethmoid, ventral ethmoid, anterior myodome bones and capsular ethmoids) will be found in some pholidophoroid. This is so, but they are not separate ossifications. The endochondral bone of the mesethmoid in leptolepids and pholidophorids is surrounded by continuous perichondral bone, whose upper, lower and lateral surfaces are respectively homologues of the supraethmoid, ventral ethmoid and capsular ethmoids. I have not yet seen an anterior myodome bone in any leptolepid, but one is present as a hollow cone of perichondral bone on the posterior surface of the mesethmoid in *Pholidophorus germanicus* (Lower Jurassic) and *P. macrocephalus* (Upper Jurassic).

In summary, the evidence is that the primitive condition of the ethmoid endoskeleton in teleosts is to have a median mesethmoid and paired lateral ethmoids, each well ossified in endochondral and perichondral bone. Reduction of endochondral bone

followed by reduction of perichondral bone has occurred in many lineages, in some groups resulting in several separate perichondral ossifications.

This rather lengthy preamble is necessary before the structure of the ethmoid region in *Gaudryella* and *Humbertia* can be discussed. Of the two, *Gaudryella* is the more primitive in having the dermal skeleton (rostral) and endoskeleton (mesethmoid) still separate. The rostral of *Gaudryella* (Fig. 2) is strikingly like those of *Leptolepis* (Fig. 34) and *Megalops* (Fig. 35A), and I have little doubt that the lateral processes of the rostral in the three, though slightly different in form, are homologous.

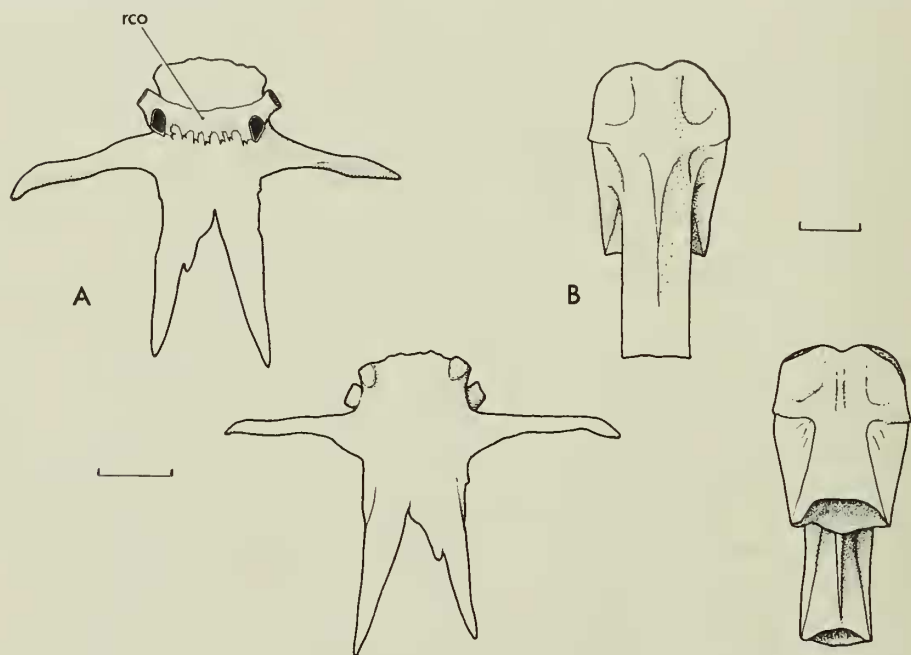


FIG. 35. A, *Megalops cyprinoides* (Broussonet), rostral of a 90 mm. individual in dorsal (above) and ventral view, 1855.9.19.832. B, *Argentina sialis* Gilbert, mesethmoid of a 72 mm. individual in dorsal (above) and ventral view, same specimen as Fig. 29A. Scale 1 mm.

Gaudryella is more advanced than *Leptolepis* and *Megalops* in having no impression on the bone of the ethmoid commissure or pit-line, but is more primitive than *Megalops* in having a well ossified mesethmoid below the rostral, and more primitive than most leptolepids in having the rostral and mesethmoid unfused. Apart from the loss or reduction of the ethmoid commissure, therefore, the ethmoid region of *Gaudryella* is one of the most primitive known amongst teleosts. All euteleosteans are more advanced in this region, and even those which still retain separate rostral and mesethmoid ossifications (coregonines, esocoids, osmerids, some stomiatooids) have the mesethmoid poorly ossified and the rostral (or proethmoids) usually short and plate-like. The proethmoids of the stomiatooid *Polymetme* (Weitzman 1967b,

fig. 12) are reminiscent of the anterior part of the rostral of *Gaudryella*, and the proethmoids of some esocoids extend back over the frontals like the rostral of *Gaudryella*, but there seem to be no other similarities worth comment. Although the ethmoid ossifications of *Gaudryella* are too primitive to be readily compared with those of any euteleostean, this does not mean that the fish may not be related to some living group in which these ossifications are more advanced.

In *Humbertia* the body of the mesethmoid (Fig. 16) is rather similar to the endoskeletal mesethmoid of *Gaudryella* but less heavily ossified, while the long, membranous posterior processes are presumably the homologues of the posterior processes of the rostral in *Gaudryella*, although in *Humbertia* they lie below, not above the frontals. In having the dermal and endoskeletal components of the ethmoid ossification fused, *Humbertia* is more advanced than the coregonines, esocoids, osmerids and primitive stomiatoids, in which the two remain separate, while in the rather flimsy, lightly ossified mesethmoid *Humbertia* is more advanced than generalised ostariophysans and neoteleosts. Among primitive euteleosteans, the closest approach to the mesethmoid of *Humbertia* seems to be in *Argentina* (Fig. 35B), where the degree of ossification and the shape are very similar, except that the long posterior processes are lacking.

(ii) *Jaws and dentition*

In *Gaudryella* the vomer is toothed, the palatine and premaxilla are toothless, the premaxilla is short and has no distinguishable articular and ascending processes, the dentary is toothed only near the symphysis, and the basihyal is toothed. In *Humbertia* the vomer and basihyal are toothless, the palatine and premaxilla are toothed, the premaxilla is rather long and has rudimentary articular and ascending processes, and the dentary has blade-like teeth along most of its oral border. Also, *Humbertia* has rather large pharyngeal teeth but pharyngeal teeth have never been seen in *Gaudryella*. These rather profound differences, like those in the ethmoid region, are surely correlated with different feeding methods, although it is not possible to speculate on the different habits involved. But the differences in the dentition suggest that *Gaudryella*, with its few teeth placed on or near the mid-line, has the primary bite between the toothed vomer and tongue, as in argentinoids and coregonines, while *Humbertia* has a primary grasping or holding bite between the toothed dermal upper and lower jaws, and a secondary gulping bite between the pharyngeals, as in myctophiforms and higher teleosts.

The simple, toothless premaxilla of *Gaudryella* (Fig. 7A) resembles those of the argentinoids, but is even simpler than these (Fig. 36A), which have at least a distinct articular process (arpm). The premaxilla of *Humbertia* (Fig. 23) is very like those of osmerids, especially *Hypomesus* (Fig. 36B). The maxillae and supramaxillae of *Gaudryella* and *Humbertia* are very similar, and are so primitive (cf. elopoids, clupeoids) that little can be said of them. The only other euteleosteans with two supramaxillae are the alepocephaloids, some stomiatoids, and primitive neoteleosts.

The lower jaw is similar in shape in *Gaudryella* (Fig. 8) and *Humbertia* (Fig. 22A), with a long, steeply ascending coronoid process, concave anteriorly. A coronoid process of this type has been used by palaeontologists as a character of various taxa and as evidence of various supposed phyletic lines. Dr. P. H. Greenwood has sug-

gested to me that a lower jaw of this type may be merely a 'grade' character, presumably adaptive, in primitive teleosts. This interpretation is certainly supported by the distribution of this type of mandible, which is found in *Ichthyokentema*, *Leptolepis*, *Allothrissops*, *Pachythrissops*, *Clupavus*, *Ctenothrissa*, some clupeoids, *Coregonus*, *Hypomesus*, *Chanos*, some cyprinoids, etc., the dentition ranging from bands of small teeth along the whole oral border (*Pachythrissops*) to nothing (*Chanos*, *Clupavus*, cyprinoids). It is clear from this list that the shape of the lower jaw can hardly be used as evidence of relationship. In *Gaudryella* the mandibular dentition is much reduced, as in some *Leptolepis*, *Coregonus* and *Hypomesus* (Fig. 37B). The mandibular dentition of *Humbertia* (Fig. 24), with small anterior teeth and a short diastema followed by a series of blade-like, serrated teeth, is very unusual. The closest approach to it seems to be among the argentinoids, where the mandibular teeth are blade-like, in a single row, and apparently fused to the bone in microstomatines, and in *Bathylagus* (Fig. 37A) are similar but show a progressive increase in size from front to rear, with traces of serration on the larger posterior teeth.

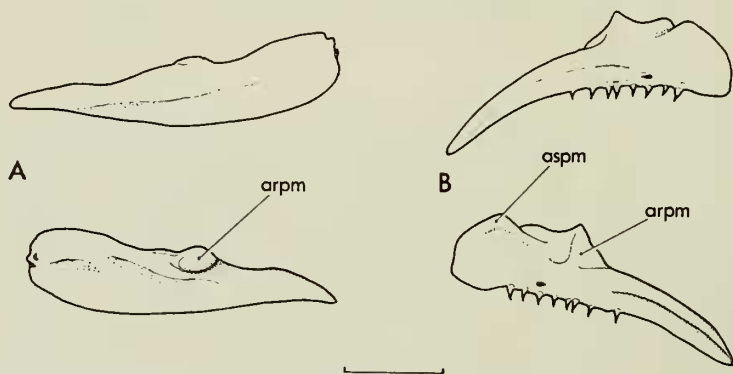


FIG. 36. Right premaxillae in external (above) and internal view of A, *Argentina sialis* Gilbert, Recent, N.E. Pacific, 1967.3.5.2, 87 mm. ; B, *Hypomesus olidus* (Pallas), Recent, same specimen as Fig. 29B. Scale 1 mm. Explanation of abbreviations p. 296.

Weitzman (1967b : 529) has drawn attention to the recess on the inner face of the dentary which houses the anterior end of Meckel's cartilage and the angulo-articular, and the insertion of the adductor mandibulae muscle. He concludes that a large recess, opening far back, as in some osmeroids and stomiatoids, is primitive for teleosts. Weitzman notes that the recess is small or absent in galaxioids, salmonids and esocoids, but large and posterior in some alepocephaloids, myctophoids, and in *Elops* and *Megalops*. Among early fossil teleosts, the pholidophorids, which have a somewhat *Amia*-like mandible, have no such recess in the dentary. *Leptolepis coryphaenoides* and other early leptolepids have a very minute recess, about as in *Humbertia* (Fig. 22A), while the Upper Jurassic *L. dubius* has a slightly larger recess. The Upper Jurassic *Anaethalion*, which is very similar to *Elops* (Nybelin 1967b), has a much smaller recess than *Elops* : in the best preserved *Anaethalion* specimen available to me the recess opens at a point distant from the symphysis by 28% of the total

length of the mandible, while in *Elops* it opens almost exactly midway along the mandible. This evidence indicates that the recess on the inner face of the dentary is a structure which has appeared within the teleosts, and that a small, anteriorly placed recess is therefore primitive. The large, posteriorly placed recess of osmeroids and stomiatoids would then be another advanced character indicating that the two groups are related. *Hypomesus* (Fig. 37B), however, is an osmerid with a small, anteriorly placed recess. The recess is extremely small in *Humbertia*, resembling that of early leptolepids, and is probably primitive. *Gaudryella* has a fairly large recess, about as in *Argentina* among argentinoids, *Mallotus* among osmerids.

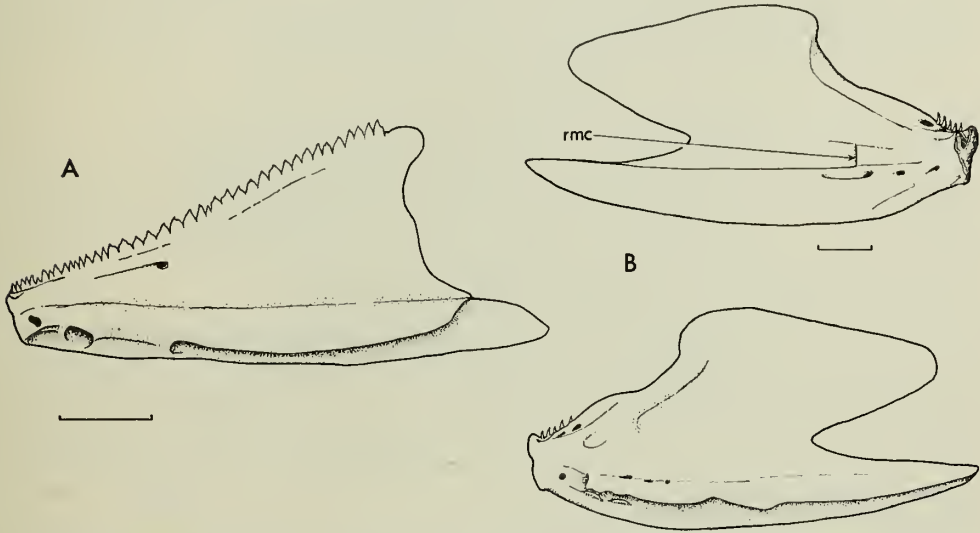


FIG. 37. Left dentaries of A, *Bathylagus antarcticus* Günther in lateral view, Recent, 'Discovery' station 298, 85 mm. ; B, *Hypomesus olidus* (Pallas) in medial (above) and lateral view, same specimen as Fig. 29B. Scale 1 mm. rmc, recess housing Meckel's cartilage.

In the palate, *Gaudryella* and *Humbertia* differ from osmeroids, stomiatoids and galaxioids in the complete absence of endopterygoid teeth. The lack of ectopterygoid teeth in *Gaudryella* and *Humbertia* is typical of salmoniforms : amongst euteleosteans, ectopterygoid teeth occur only in neotelosts and in a few characoids (Weitzman 1967b : 529). The metapterygoid of *Humbertia* is normal and unremarkable, but the reduced metapterygoid of *Gaudryella* resembles that bone in argentinoids (Chapman 1948).

The shaft of the vomer is probably primitively moderately long, as it is in *Pholidophorus germanicus*, *Leptolepis* (Patterson 1967b, fig. 5 ; and observations on other species), *Elops*, *Alepocephalus*, etc. The very long shaft seen in argentinoids, *Gaudryella* and *Humbertia* and the complete absence of a shaft in osmerids, *Retropinna*, *Prototroctes*, etc., are probably divergent specialisations which tend to align *Gaudryella* and *Humbertia* with the argentinoids.

Restriction of teeth to the margin of the basihyal tooth plate in *Gaudryella* is a feature typical of salmonoid, argentinoid, osmeroid and galaxioid salmoniforms, but not of stomiatoids or esocoids (Nelson 1970). In lacking a dermal basihyal plate, *Humbertia* differs from primitive members of all these groups.

In summary, the jaws and palate of *Gaudryella* and *Humbertia* are closest to those of argentinoids, especially in the long vomer and toothless endopterygoid of both genera, the premaxilla and reduced metapterygoid of *Gaudryella*, and the mandibular dentition of *Humbertia*. But neither genus shows the marginal vomerine teeth and elongate basihyal tooth plate which are so characteristic of argentinoids. Apart from the features mentioned here, the jaws and palate of *Gaudryella* and *Humbertia* are too generalised to be much help in deciding on relationships. Although there are marked differences between the two genera in the jaws and palate, I cannot find that these show one genus to be closer to any group than is the other.

(iii) *Hyoid and branchiostegals*

In the perforate ceratohyal, *Gaudryella* and *Humbertia* are more primitive than any known euteleosteans except *Coregonus* (Fig. 28) and some neoteleost groups (ctenothrissiforms, primitive paracanthopterygians and acanthopterygians). But the fenestra in the ceratohyal has been lost independently in many groups and no particular significance can be attached to it.

The two ossifications of the ceratohyal are separated by cartilage in *Gaudryella*, as they are in all primitive teleosts according to McAllister (1968, table 1). In *Humbertia* the two ossifications are sutured together by splints on their inner faces. McAllister finds this to be an advanced character, independently acquired in siluroid ostariophysans and in neoteleosts, where it first occurs in *Ctenothrissa*, is absent in beryciforms and commonly occurs in both acanthopterygians and paracanthopterygians. I cannot see that the suture in *Humbertia* is anything but a further example of independent acquisition of the feature.

Gaudryella has eleven branchiostegals, all slender and almost straight (acinaciform) except for the last two, which are spathiform and curved distally (Fig. 32A). *Humbertia* has seven or eight branchiostegals of which the last five are broad and spathiform, the last two being especially broad and strongly curved, with 'clupeoid projections' at their bases (Fig. 32B). The distribution of spathiform branchiostegals (McAllister 1968, table 1) shows that this is undoubtedly the primitive condition in actinopterygians, while 'clupeoid projections', which occur in clupeoids, bathylaconids (Alepocephaloidei), osmerids, chanoids, characoids and cyprinoids, seem to be a character of primitive teleostean groups in which the branchiostegal number is low. The pattern of the branchiostegals in *Gaudryella* and *Humbertia* is similar to those of argentinoids, osmeroids, stomiatoids and galaxioids. *Gaudryella* has more numerous branchiostegals than argentinoids (2-7), osmeroids (4-10) and galaxioids (3-9), but fewer than many stomiatoids (5-24). The branchiostegals of stomiatoids are shorter than those of *Gaudryella*, those of galaxioids are straighter. In general, the branchiostegals of *Gaudryella* seem closest to those of osmerids. *Humbertia* has fewer branchiostegals than some osmeroids, stomiatoids and galaxioids. In number and shape of the branchiostegals *Humbertia* is close to *Argentina* (7 rays), but the last rays

of this genus are neither so broad nor so strongly curved as in *Humbertia*. The osmeroid *Plecoglossus* (6 rays) has very broad, crescentic posterior branchiostegals, as in *Humbertia*.

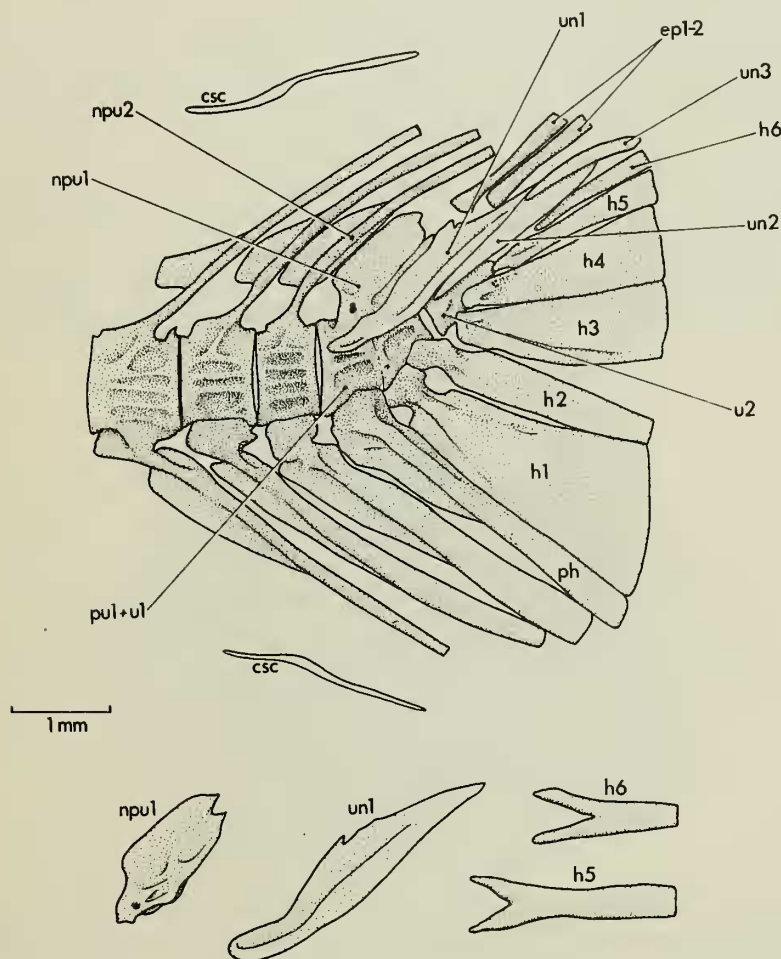


FIG. 38. *Argentina sialis* Gilbert, Recent. Above, caudal skeleton of a stained and cleared specimen (same specimen as Fig. 36A) ; below, detached bones of a macerated specimen from the same lot (same specimen as Fig. 29A), the first pre-ural neural spine and first uroneural in lateral view (the neural spine broken from the centrum), the fifth and sixth hypurals in dorsal view. Explanation of abbreviations p. 296.

(iv) Caudal skeleton

As noted above, fusion of the first pre-ural and ural centra is known only in the argentinoids, galaxioids, osmeroids, stomiatoids, ostariophysans and neoteleosts. Caudal structures in these groups will be discussed in relation to the conditions in *Gaudryella* and *Humbertia*.

Amongst argentinoids, caudal skeletons have been illustrated in *Opisthoproctus* (Trewavas 1933, pl. 2 ; Parr 1937, fig. 13), *Bathylagus* (Beebe 1933, fig. 41), *Macropinna* (Chapman 1942a, fig. 6), *Nansenia* (Chapman 1948, fig. 12) and *Argentina* (Gosline 1960, fig. 10 ; Rosen & Patterson 1969, fig. 71). *Microstoma*, *Bathylagus* and *Argentina* are illustrated here (Figs. 38-41). In *Opisthoproctus* and *Macropinna* the illustrations by Trewavas, Chapman and Parr all seem to show separate centra supporting the parhypural and the lower hypurals, and alizarin preparations of two specimens of *Opisthoproctus* in the American Museum of Natural History show that PU1 and U1 are separate. In other argentinoids the compound centrum (PU1 + U1) is very long, as in *Humbertia* (Figs. 26, 27), and in *Argentina* there are often surface markings (Rosen & Patterson 1969, fig. 71 ; Fig. 38) suggesting that two centra have fused during ontogeny, though they are not separable, even under heavy maceration. There are six hypurals in argentinoids, as in *Gaudryella* and *Humbertia*, and there is a free second ural centrum in *Argentina* (Fig. 38), *Microstoma* (Fig. 39), *Macropinna* and

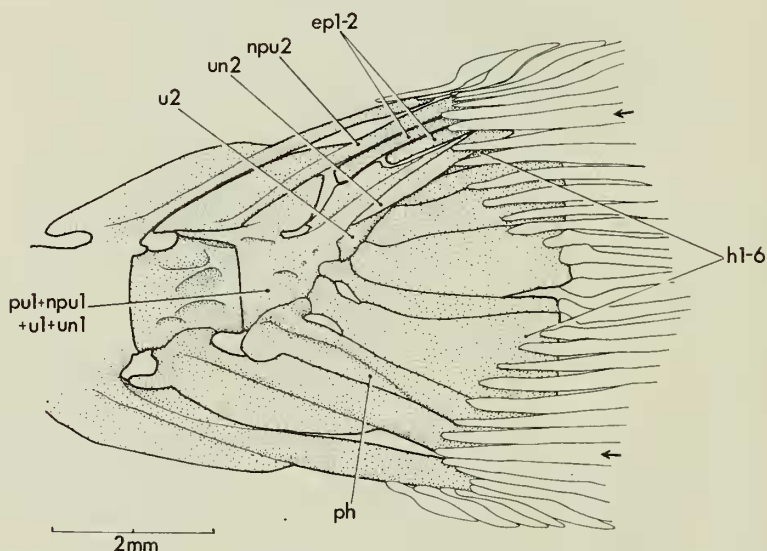


FIG. 39. *Microstoma microstoma* (Risso), Recent. Caudal skeleton of a dried skeleton, 1888.11.29.67, 150 mm., Mediterranean. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

Bathylagus (Fig. 41), where it is much reduced and not visible externally. In *Nansenia* Chapman's figure shows no U2, but dissected specimens have a small one, much as in *Bathylagus*. *Argentina*, *Bathylagus*, *Microstoma* and *Opisthoproctus* have a full neural spine on PU2, but in *Macropinna* and *Nansenia* Chapman's illustrations show a low, broad neural spine, as in *Gaudryella* and *Humbertia*. However, in two dissected specimens of *Nansenia groenlandica* there is a full neural spine on PU2, and since other features lead one to mistrust Chapman's drawings of caudal skeletons it appears that a full neural spine on PU2 is characteristic of argentinoids. All argentinoids have two or fewer epurals. In *Argentina* there are three uroneurals, large

caudal scutes, and a urodermal (Rosen & Patterson 1969, fig. 71). *Opisthoproctus* also has a urodermal (D. E. Rosen, pers. commn.). *Bathylagus* (Fig. 40) also has three uroneurals, but no caudal scutes or urodermal, and the first uroneural is fused with the supporting compound centrum. In *Microstoma* (Fig. 39) there are only two uroneurals, the first fused with the compound centrum. The illustrated specimen of *Microstoma* is of interest in having the first uroneural produced forwards across PU2, as it is in *Gaudryella* and *Humbertia*, but this projection

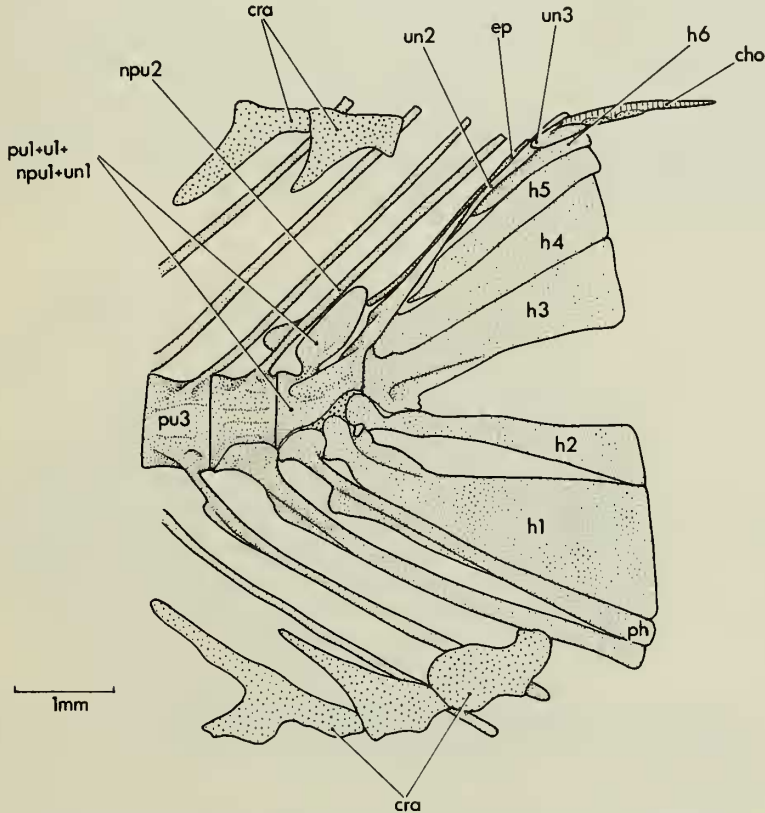


FIG. 40. *Bathylagus antarcticus* Günther, Recent. Caudal skeleton of a dissected specimen, 100 mm., same lot as Fig. 37A. *cho*, notochord; *cra*, cartilages supporting the procurrent caudal rays (the last upper cartilage removed); explanation of other abbreviations p. 296.

is missing on the right side of the specimen. In *Bathylagus* and especially in *Microstoma* fusion of the first uroneural with the compound centrum produces a caudal skeleton resembling that of *Gaudryella* (Figs. 13, 14), but the caudal skeleton of *Argentina* disposes of this apparent similarity. Gosline's figure (1960, fig. 10) of a large dried skeleton of *Argentina silus* (standard length c. 33 cm.) shows a suture

between the first uroneural (UN₁) and the neural arch of the compound centrum (NA). Maceration of a 75 mm. specimen of *A. sialis* (Fig. 38) shows that this is correct: the first uroneural (un₁) is quite separate from the neural arch (np_{u1}), which is fused with the compound centrum. In *Bathylagus*, although the lower part of the first uroneural is fused with the compound centrum, the neural arch of that centrum (which may be double, Fig. 41) is quite distinct from the uroneural. This shows that in argentinoids the neural arch of the compound centrum, NP_{U1} (or NP_{U1} and NU₁ where the arch is double) fused first with the centrum, not with the first uroneural. Argentinoids therefore never had a true stegural, taking the stegural to be the first uroneural fused with the neural arches of PU₁ and U₁ (Patterson 1968a : 229 ; 1968b : 50). The implications of this are discussed further below, but it immediately excludes the argentinoids from relationship with *Gaudryella* and *Humbertia*, in which a stegural of normal type occurs. Since PU₁ and U₁ are still separate in *Opisthoproctus* (and possibly also in *Macropinna*) it is likely that all early argentinoids had these centra separate, and were also more primitive than *Gaudryella* and *Humbertia* in this feature.

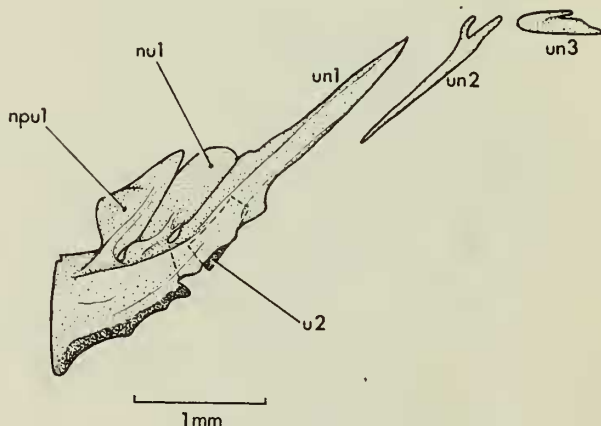


FIG. 41. *Bathylagus antarcticus* Günther, Recent. Dissociated parts of the caudal skeleton of a stained and macerated individual, same specimen as Fig. 37A. Explanation of abbreviations p. 296.

In the osmeroids and stomiatoids the caudal skeleton is similar. In osmeroids it has been illustrated in *Osmerus* (Berg 1955, fig. 198), *Thaleichthys* (Chapman 1941, fig. 15), *Hypomesus* (Gosline 1960, fig. 5), *Spirinchus* (Weitzman 1967b, fig. 4) and *Plecoglossus* (Gosline 1960, fig. 12). *Osmerus* and *Hypomesus* are illustrated here (Figs. 42, 43). All have no free second ural centrum, the parhypural and six auto-genous hypurals articulating with a single upturned centrum, and the stegural is fused with this centrum (pu₁ + u₁ + u₂ + st). The stegural has a deep notch in its anterior margin, marking the cleft between the neural arch and uroneural components, as in *Gaudryella* and *Humbertia*. All osmeroids have two epurals, as in argentinoids and *Gaudryella* (the dried skeleton of *Hypomesus* illustrated by Gosline

has two epurals, not one as shown), and there are independent second and third uroneurals (un2, un3), as in *Humbertia*. There is a urodermal in *Osmerus* (Patterson 1968a : 230 ; Fig. 42) and *Hypomesus* (Fig. 43), but caudal scutes are absent (Weitzman 1967b : 532). The neural spine of PU2 is short, as in *Gaudryella* and *Humbertia*, in all published illustrations of osmeroid tails (Gosline's individual of *Hypomesus* is abnormal in having two neural spines, one long and one short, on PU2 ; cf. Fig. 43). In *Osmerus*, Berg illustrates short neural spines on both PU2 and PU3, a most unusual condition, while in the three dried skeletons of *O. eperlanus* available to me, one (npu2, Fig. 42) has a short neural spine on PU2 and the other two have full neural spines. In general, osmeroids show a combination of primitive features (NPU2 short, three uroneurals, hypurals autogenous) and advanced features (no free U2, stegural fused with compound centrum and with no extension forward to PU2, two epurals, no caudal scutes) which distinguish them from both *Gaudryella* and *Humbertia*, but a *Humbertia*-like caudal skeleton could well be antecedent to the osmeroid type.

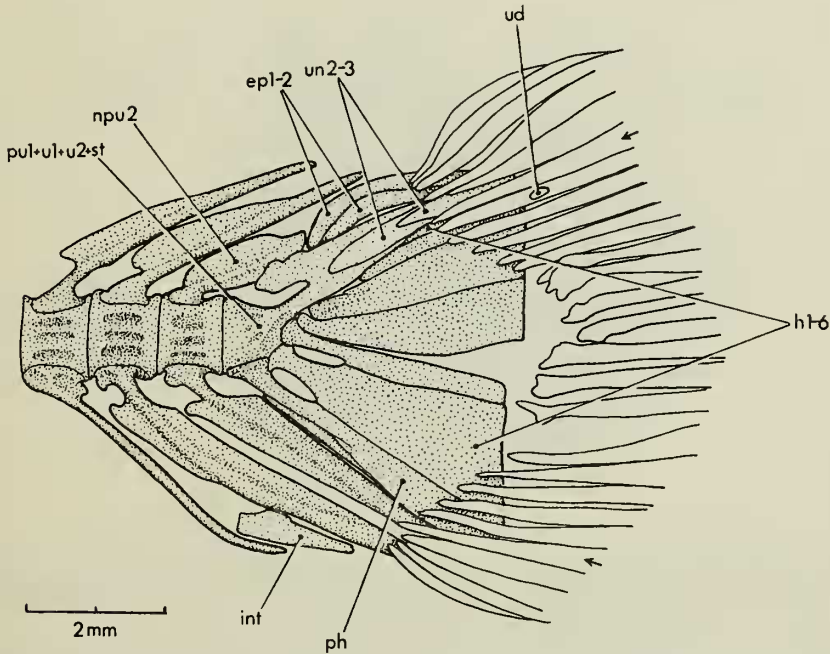


FIG. 42. *Osmerus eperlanus* (L.), Recent. Caudal skeleton of a dried skeleton, BM(NH) unreg., 100 mm., Berlin. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

In stomiatoids, which Weitzman places as the closest relatives of osmeroids, the caudal skeleton is known in *Polymetme*, *Vinciguerria* (Weitzman 1967b, figs. 15, 10), *Gonostoma*, *Maurolicus* (Monod 1968, figs. 393, 394 ; Weitzman 1967a, fig. 31), *Photichthys* (Gosline 1960, fig. 9) (all Gonostomatidae, the most primitive family according to Weitzman), *Astronesthes*, *Borostomias* (Weitzman 1967a, figs. 14, 31 ;

both *Astronesthidae*), *Chauliodus* (Monod 1968, fig. 396 ; *Chauliodontidae*) and *Idiacanthus* (Beebe 1934, figs. 74, 78 ; *Idiacanthidae*). A free second ural centrum is present in *Polymetme*, *Borostomias antarcticus* and possibly in *Maurolicus*, and in this the stomiatooids are more primitive than osmeroids. In *Polymetme* and *Gonostoma* there are six autogenous hypurals, but in other forms there may be only five (*Photichthys*, *astronesthids*, *Chauliodus*) or there are various fusions. In *Maurolicus* and *Vinciguerria* hypurals 1 + 2 and 3 + 4 are fused, and there are two slender, autogenous hypurals above, as in *Gaudryella*, while *Vinciguerria* has these two hypural plates and the parhypural fused with the compound centrum. *Borostomias*, *Polymetme* and *Photichthys* have an autogenous stegural of typical shape, but the stegural is fused with the centrum in other genera. There is a second uroneural

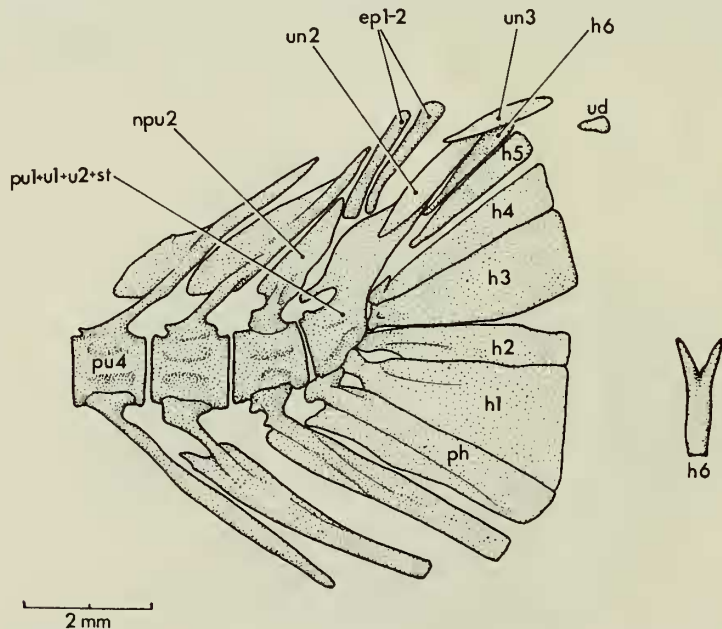


FIG. 43. *Hypomesus olidus* (Pallas), Recent. Caudal skeleton of a stained and macerated individual, same specimen as Fig. 29B. On the right is the detached sixth hypural in dorsal view. Explanation of abbreviations p. 296.

in all genera except *Polymetme* and *Chauliodus*, but none has a third. There are three epurals in *Gonostoma*, two or one in other genera. All stomiatooids have a full neural spine on PU₂, and in this they are more advanced than osmeroids, *Gaudryella* and *Humbertia*. No stomiatooid is known to have caudal scutes or a urodermal. There is clearly a wide range of caudal structure in stomiatooids, and no one genus can be clearly characterised as more primitive than the others. The occurrence of a second ural centrum, an autogenous stegural and three epurals in some forms shows that the stomiatooid caudal skeleton cannot be derived from the osmeroid type.

Fusions between the hypurals and centra in some stomiatooids are similar to those in *Gaudryella*, but the tail of *Gaudryella* is more primitive in several ways and any direct relationship is unlikely. As in the osmeroids, however, a *Humbertia*-like caudal skeleton could be antecedent to that of stomiatooids.

Among galaxioids, the caudal skeleton has been illustrated in *Galaxias* (Gosline 1960, fig. 11 ; McDowall 1969, fig. 4B), *Brachygalaxias* (Greenwood *et al.* 1966, fig. 4C) (both Galaxiidae), *Aplochiton* (Chapman 1944, fig. 10 ; McDowall 1969, fig. 4C), *Lovettia* (McDowall 1969, fig. 4D) (both Aplochitonidae *sensu* McDowall), *Prototroctes* (McDowall 1969, fig. 4E ; Prototroctidae), and *Retropinna* (McDowall 1969, fig. 4A ; Retropinnidae). *Galaxias brevipinnis* is illustrated here (Fig. 44).

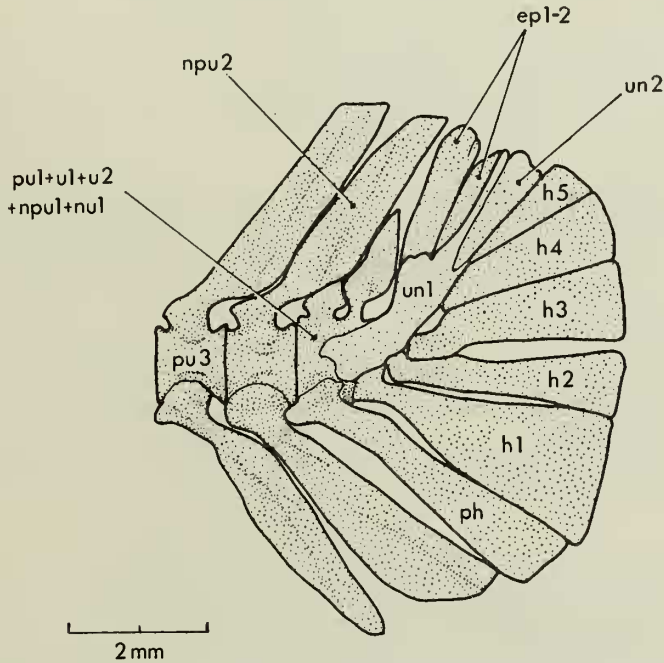


FIG. 44. *Galaxias brevipinnis* Günther, Recent. Caudal skeleton of a dried skeleton, BM(NH) unreg., 105 mm., New Zealand. Explanation of abbreviations p. 296.

McDowall has recently (1969) made an osteological investigation of the galaxioids and finds that they fall into two groups (at present unnamed), one containing the Retropinnidae and Prototroctidae, the other the Galaxiidae and Aplochitonidae. This separation is shown very clearly by the structure of the caudal skeleton. In *Retropinna* and *Prototroctes* (dried skeletons of *Prototroctes oxyrhynchus* and *Retropinna* sp. examined) the caudal skeleton is similar, with six hypurals, the four upper ones autogenous, the two lower ones more or less fused with the parhypural (cf. *Gaudryella*), a low, broad neural spine on PU2 (as in *Gaudryella*, *Humbertia* and most osmeroids), three epurals, a large stegural with a deep notch in

its anterior margin (again as in *Gaudryella*, *Humbertia* and osmeroids), a second uroneural, and 16 branched caudal rays. In some populations of *R. retropinna* McDowall reports a small second ural centrum, but in most *Retropinna* and in *Prototroctes* there is no U2. The stegural appears to be autogenous in the dried skeletons I have examined and in McDowall's figures, but in *Retropinna* he describes it as 'more or less ankylosed' to the compound centrum. This caudal skeleton is strikingly like those of the osmeroids, differing only in the partial fusion of the parhypural and the lower hypurals, the three epurals, the absence of a third uroneural, and the autogenous stegural, all features which occur in the stomiatoids. The caudal skeletons of *Retropinna* and *Prototroctes* are also very like that of *Gaudryella*.

The galaxiids and aplochitonids have only five hypurals, a neural spine on PU2 which is often double but usually (? always) complete, two or less epurals, two uroneurals of which the first is autogenous in Gosline's and McDowall's specimens (see also Fig. 44), but is fused with the centrum in the BM(NH) dried skeletons of *Galaxias platei* and *Aplochiton zebra*, and 14 or less branched caudal rays. In *Brachygalaxias* there is a second ural centrum. A most important feature of all galaxiids and aplochitonids is the presence of one or two neural arches with variously developed neural spines on the compound centrum. These neural arches are often fused with the underlying centrum (Fig. 44) but are quite distinct from the first uroneural. The galaxiids and aplochitonids appear never to have developed a stegural, the neural arches of PU1 and U1 fusing with the centrum, not the uroneural, as in argentinoids (see above). This would exclude them from close relationship with *Gaudryella* and *Humbertia*, and whereas the caudal skeletons of *Prototroctes* and *Retropinna* resemble those of the osmeroids, stomiatoids, *Gaudryella* and *Humbertia*, those of galaxiids and aplochitonids resemble those of argentinoids (cf. Figs. 38-41, 44). These differences suggest that the galaxiid-aplochitonid assemblage and the retropinnid-prototroctid assemblage may not be so closely related as is generally assumed.

In primitive euteleostean fishes it seems that there are two alternative methods of incorporating the neural arches of the first pre-ural and ural centra. The first method is to fuse the paired halves of these arches with the first uroneurals, which acquire dorso-medially directed flanges and become typical stegurals: there is then no sign of arches on the underlying centrum. The 'type' stegural is that of the salmonids (see illustrations in Norden 1961; Vladykov 1962; Monod 1968). A similar stegural occurs in esocoids, osmeroids, stomiatoids, prototroctids, retropinnids, and the neoteleosts. The second method is for the neural arches of PU1 and U1 to remain separate or to fuse with the underlying centrum, the first uroneural being unmodified. This is characteristic of the alepocephaloids (including the Bathylaconoidei, Nielsen & Larsen 1968; Gosline 1969), argentinoids, galaxiids and aplochitonids.

In gonorynchiforms and ostariophysans, the only euteleosteans not yet mentioned, the caudal skeleton is greatly simplified by fusion, even in the most primitive forms (*Chanos*, Monod 1968, fig. 113; the Cretaceous gonorynchid *Charitosomus*, Fig. 45; and various ostariophysans illustrated by Monod 1968). But the configuration of

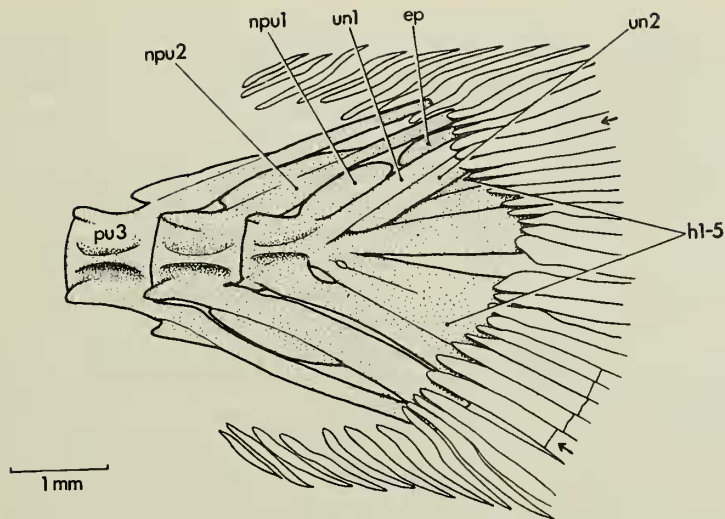


FIG. 45. *Charitosomus hakelensis* Davis, Middle Cenomanian, Hakel, Lebanon. Restoration of caudal skeleton based on P.13897. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

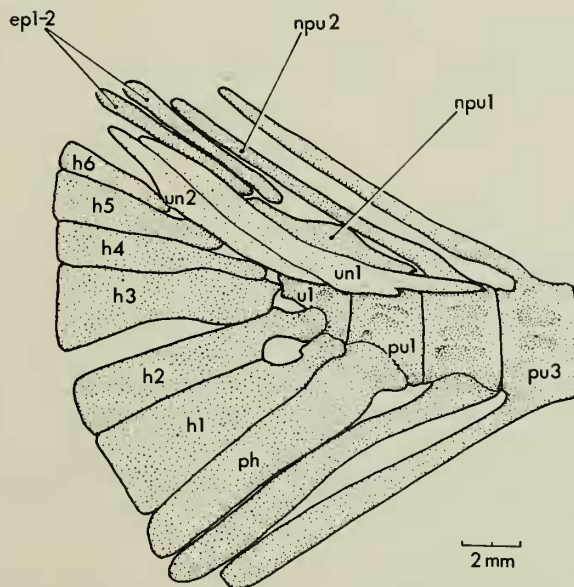


FIG. 46. *Tharrhias araripis* Jordan & Branner, Santana Formation (? Albian), Serra do Araripe, Brazil. Restoration of caudal skeleton based on specimens in a private collection. Explanation of abbreviations p. 296.

the element labelled 'ANPr' by Monod in *Gonorynchus* and ostariophysans (see especially figs. 465, 468–470) is such that I agree with Monod that it is a neural arch, not part of a stegural. In the specimen of *Chanos* illustrated by Monod this element is very small, but in each of five small individuals that I have examined it is much as in *Charitosomus* (npur, Fig. 45). Since this element is fused with the compound centrum in all ostariophysans, as is the first uroneural, it is impossible to be certain of its homologies. There are several Lower Cretaceous genera which are supposed to be relatives of *Chanos* (*Prochanos*, *Parachanos*, *Chanopsis*, *Dastilbe*, *Tharrhias*; Santos & Valenca 1968). Amongst these, the caudal skeleton is known in *Parachanos* (Arambourg & Schneegans 1936, fig. 5), *Dastilbe* (Santos 1947, figs. 5, 6) and *Tharrhias* (Fig. 46). In all these it is very similar, with PU1 and U1 separate, six autogenous hypurals, a full neural spine on PU2, two (or less) epurals, and two uroneurals, the first of which extends forwards across PU2. Probably, all have a small U2, hidden below the second uroneural (U2 is visible in one specimen of *Dastilbe* where the second uroneural is displaced). Between the first uroneurals and above PU1 and U1 there is a separate, elongate bone (labelled 'na' by Arambourg & Schneegans; npur in Fig. 46) which must represent the neural arch of PU1 (cf. *Albula*, Monod 1968, figs. 96–103). If these Lower Cretaceous fossils are really relatives of *Chanos* (which is not possible to prove at present, but is likely because of the structure of the jaws and cheek, the enlarged first rib, and other features) separation of the first uroneural and the neural arch of PU1 is further evidence that the gonorynchiforms and ostariophysans never developed a stegural, and provisionally they can be included with the other euteleosteans of this type.

Fig. 47 is modified from Gosline's (1960) diagram 2, incorporating information from the caudal skeleton only. Whether this is a valid scheme is debatable, but at least it offers some testable hypotheses. On present evidence, *Gaudryella* and *Humbertia* fall with the osmeroids, stomiatoids and retropinnids, as shown.

(v) *Conclusions*

Despite many resemblances to the argentinoids, both general (p. 254) and particular (reduced dentition, long vomer, ethmoid of *Humbertia*, premaxilla of *Gaudryella*, etc.) any close relationship between *Gaudryella* or *Humbertia* and the argentinoids is excluded by the cellular skeleton, absence of a true stegural, and occasional presence of separate PU1 and U1 in argentinoids (Fig. 47). Although *Humbertia* is more similar to the argentinoids than is *Gaudryella* in the ethmoid, mandibular dentition and branchiostegals, *Gaudryella* is more argentinoid-like than *Humbertia* in the toothless premaxilla, reduced metapterygoid and toothed basihyal, so that it cannot be said that either genus is closer to the argentinoids than the other. Many of the resemblances between argentinoids and the fossil genera are in primitive characters. Others, especially those in the jaws, vomer, and dentition must be regarded as parallelisms.

There is not much resemblance between either *Gaudryella* or *Humbertia* and the galaxioids (*Retropinna* and *Prototroctes* excluded), and, as in argentinoids, any close relationship is excluded by the absence of a stegural in galaxioids (Fig. 47).

As possible relatives of *Gaudryella* and *Humbertia* there remain only the osmeroids,

stomiatooids and the 'galaxioids' *Retropinna* and *Prototroctes*. Such a relationship is opposed by the long vomer and lack of endopterygoid teeth in *Gaudryella* and *Humbertia*, by the toothless premaxilla and reduced metapterygoid of *Gaudryella* and the sutured ceratohyal and toothless basihyal of *Humbertia*. But in almost every other character the differences between these living groups and the fossil genera are due to the retention of primitive characters in the latter. The best positive evidence for such a relationship is provided by the structure of the caudal skeleton.

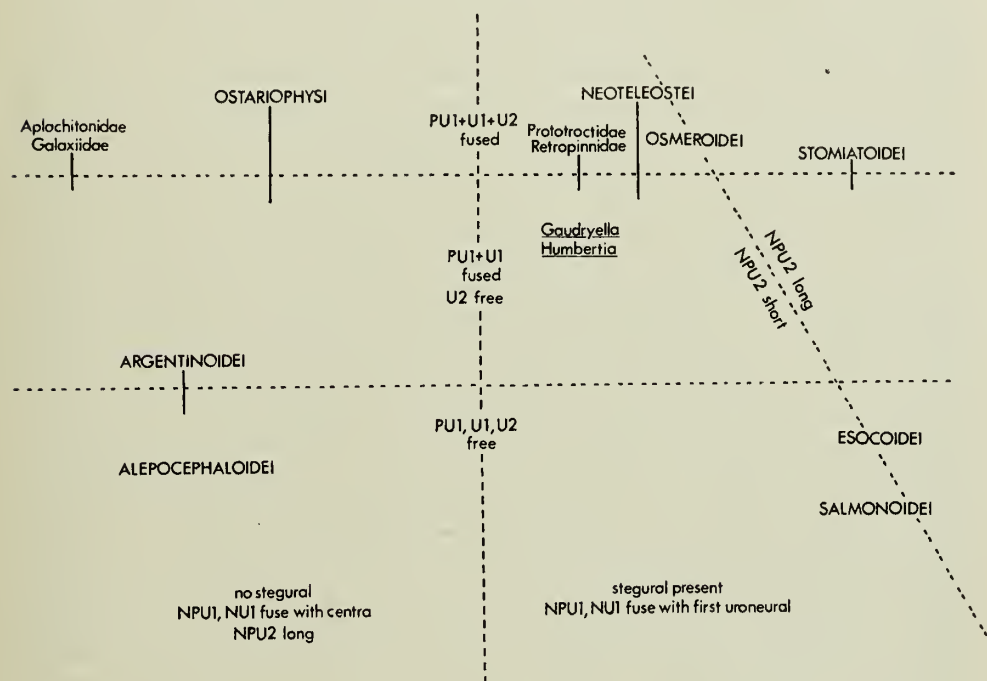


FIG. 47. Diagram showing the distribution of certain caudal structures in euteleosteans.

The solid line below certain groups indicates that some members exhibit the more primitive grade of structure. For further explanation see text.

Weitzman (1967b : 533) has constructed an archetype which could be the common ancestor of living osmerids and stomiatooids. This hypothetical proto-osmerid resembles *Gaudryella* and *Humbertia* in many ways, although the two fossil genera are more primitive in having an orbitosphenoid, a fully roofed post-temporal fossa, and various other features not listed by Weitzman. The major differences between the fossil genera and Weitzman's archetype, apart from those in the dentition, concern the ethmoid region, the shape of the palatine, and the lower jaw. The structure of these in Weitzman's archetype seems to be strongly influenced by the opinion, originating with Chapman (1941) and endorsed by McAllister (1963, 1966), that *Spirinchus* and/or *Thaleichthys* are the most primitive osmerids. The reasoning on

which these opinions are based seems to me suspect. Chapman (1941 : 297) decided that *Thaleichthys* was the most primitive osmerid because of the large amount of cartilage in the preorbital part of the braincase, the numerous ethmoid bones, and the development of membranous wings linking the pterosphenoid and prootic. In my opinion, all these are advanced characters, those of the neurocranium because of reasons given in the discussion of the ethmoid region above, those of the pterosphenoid and prootic because they involve the development of membrane bone outgrowths from primitively endochondral bones. McAllister (1963) followed Chapman in regarding *Thaleichthys* as the most primitive osmerid, but recognised two sub-families, Hypomesinae and Osmerinae, which must be of equal age, as his dendrogram (fig. 13) shows. But in 1966 McAllister published a numerical study of osmerids based on the information in his earlier conventional study, and produced a new dendrogram (1966, fig. 2) which placed *Thaleichthys* as the most primitive osmerid, below the common ancestry of Hypomesinae and Osmerinae, with *Spirinchus* as an advanced member of the Osmerinae. This reversal of the positions of *Spirinchus* and *Thaleichthys* was arrived at partly by counting the primitive characters found in each osmerid genus, and partly by computing the coefficient of association between Hypomesinae and each osmerine genus ; only the first of these procedures will be commented on here. McAllister cited 22 osmerid character states which he considered primitive. The primitive condition of each character was discovered by making two assumptions, first, that paired proethmoids are primitive, and second that salmonines are close to the ancestry of osmerids, and that characters shared by salmonines and any osmerid are therefore primitive. Neither of these assumptions is justified in my opinion. The first is discussed above (p. 259). The second leads McAllister to find that the medioparietal skull roof of *Hypomesus* is a derived condition, and that primitive osmerid characters include such things as caniniform basihyal teeth and approximately three scale rows per trunk segment (as in *Mallotus*, all other osmerids having approximately one scale row per segment). Some of the character pairs selected by McAllister for his 'primitiveness' count are such that I believe no decision is possible on which state is the more primitive (angle of mouth, place of spawning, adult size). But Chapman (1941) mentions osteological features of certain osmerid genera which can confidently be characterised as primitive, such as the anterior strut on the intercalar in Hypomesinae and *Spirinchus*, the absence of a membrane bone strut between the pterosphenoid and prootic in Hypomesinae, and the slender palatine of Hypomesinae (cf. Fig. 22B). These, and other characters suggest to me that Hypomesinae are the plesiomorph sister-group of Osmerinae, and that *Hypomesus* is the most primitive osmerid genus. Further evidence of this is provided by the almost semicircular operculum of *Hypomesus* (cf. Weitzman 1967b : 529), the small, anteriorly placed recess on the inner face of the dentary (p. 267, Fig. 37B) and the autogenous parapophyses and neural arches on the anterior vertebrae (fused with the centra in other osmerids according to Weitzman (1967b : 530)). Indeed, it seems that many of the similarities between osmerids and stomiatooids on which Weitzman (1967b) places emphasis are in fact similarities between stomiatooids and Osmerinae. This at least raises the possibility that the shallow mandible, long jaws, large gape and short ventral limb of the preopercular in

osmerines and stomiatoids are not primitive for the group. The very long jaws, caniniform teeth and posteriorly inclined, almost palaeoniscoid suspensorium of many stomiatoids are surely secondarily acquired, and one could argue that the vertical suspensorium, moderately long jaws and relatively large teeth of osmerines represent the beginning of a trend towards enlargement of the jaws and teeth from a *Hypomesus*-like (or *Humbertia*-like) ancestor. Such changes in the jaws might be correlated with changes in jaw mechanics associated with the development of a posteriorly placed recess housing the insertion of the adductor mandibulae in the dentary. One is accustomed to regard the triangular mandible and villiform teeth of such fishes as *Elops*, *Aulopus* and *Polymixia* as the primitive condition in all teleostean lineages (cf. Gosline 1959), and to think of shortening of the gape and deepening of the mandible as irreversible changes. But a small mouth and deep mandible of the type found in *Hypomesus*, *Gaudryella* and *Humbertia* are so widely distributed among primitive teleosts (p. 266) that it is tempting to see this arrangement as a necessary consequence of the jaw mechanics of primitive forms, and as being reversible in lines where some new modification of jaw mechanics occurs.

It is therefore not entirely unreasonable to regard the *Hypomesus*-like jaws of *Gaudryella* and *Humbertia* as proto-osmerid characters, and to place these fishes near the line leading to osmeroids. Precisely where *Plecoglossus* and the salangids stand in this grouping, I cannot say, but I agree with McDowall (1969 : 816, 821) that these fishes are closer to the osmerids than to any other group, and should be included in the Osmeroidei. *Plecoglossus* and the salangid available (*Leucosoma*, cf. Gosline 1960 : 339) have caudal skeletons which are entirely of osmerid type, although *Leucosoma* exhibits considerable fusion within the lower and upper hypurals, much as in *Gaudryella* (see Nelson 1970 for another view of salangid relationships). *Retropinna* and *Prototroctes* present another problem because of their southern distribution, because of certain resemblances to the galaxioids, and because their caudal skeletons are more primitive than those of osmerids in having the stegural autogenous, a second ural centrum in some, and three epurals (all characters found in stomiatoids). They have a short vomer, a low mandible of osmerine type and the osmerid cucumber smell, but no supramaxilla, no mesocoracoid and the palatine and ectopterygoid fused. I would suggest, tentatively, that they be placed in the Osmeroidei.

In summary, the only group of living fishes with which either *Gaudryella* or *Humbertia* can be aligned is that salmoniform subgroup containing the Osmeroidei (and Stomiatoidei, if Weitzman is correct). This is hardly a satisfactory solution, for *Gaudryella* and *Humbertia* are far more primitive than any member of these groups and one cannot help being impressed by various argentinoid-like features which prevent either genus from being very close to the hypothetical proto-osmerid, the common ancestor of the group. But there are strong objections to any other solution.

There remains the problem of the interrelationships of *Gaudryella* and *Humbertia* (the size of the 'gap' between them). The differences between the two genera (Table 3) are such that if they were living fishes one would hardly place them in the same family, and the significance of these differences is increased by the age of the fossils, for in middle Cretaceous times the differences between what are now sharply distinct

groups were small (e.g. myctophiforms, paracanthopterygians and acanthopterygians ; Rosen & Patterson 1969). But I can find no convincing evidence that either genus is closer to any living group than the other, and have no reason to separate them on these grounds. Among fishes contemporary with *Gaudryella* and *Humbertia*, where most comparisons are admittedly useless because of lack of information on other forms, the same conclusion is reached (see below), and despite the trenchant differences between *Gaudryella* and *Humbertia* I am forced to regard them as each other's closest known relatives. Under these circumstances, the erection of a monotypic family for each genus would be meaningless, especially since there exists no named higher taxon (except Salmoniformes) in which to place them.

The superorder Protacanthopterygii of Greenwood *et al.* (1966) has been shrinking rapidly as various component groups are hived off into other taxa. With the removal of the myctophoids, ctenothrissiforms, and most of the cetomimiforms to the Neoteleostei (McAllister 1968 ; Rosen & Patterson 1969) and the removal of the gonorynchiforms to the Ostariophysi (Rosen & Greenwood 1970), the superorder Protacanthopterygii is now an 'empty category', containing only the order Salmoniformes (including the Giganturoidei, Rosen & Patterson 1969 : 455). Rosen & Greenwood removed the gonorynchiforms from the Protacanthopterygii because they felt that the group would otherwise be paraphyletic. But even after these fishes have gone, there is almost no evidence that the remaining protacanthopterygian group, the Salmoniformes, is monophyletic (absence of ectopterygoid teeth seems the only advanced character common to all salmoniforms). Despite recent detailed anatomical work on four of the eight salmoniform suborders (osmeroids and stomiatoids, Weitzman 1967a, b ; alepocephaloids, Gosline 1969 ; galaxioids, McDowall 1969) there is still no coherent picture of relationships among these groups. Not even Weitzman's demonstration of osmeroid-stomiatoid relationships can be regarded as well founded (Nelson 1970), and we are no nearer an understanding of the closest relatives of, for example, the salmonoids, esocoids or argentinoids. Discussions of salmoniform interrelationships by Gosline (1969) and McDowall (1969) suggest that at this level we have run out of characters on which to sort out these groups. The present investigation has produced nothing new in the skull which might be useful here, but there is one feature of the caudal skeleton which seems promising, the fate of the neural arches of the first pre-ural and ural centra. This character (Fig. 47) suggests that salmoniforms might fall into two groups, the first containing alepocephaloids, argentinoids and galaxioids (less prototroctids and retropinnids), the second containing salmonoids, esocoids, osmeroids and stomiatoids (I can find no information on these structures in giganturoids). Goody (1969) has erected four extinct salmoniform suborders containing rather specialised Cretaceous fishes : of these, the Ichthyotringoidei fall in the first group (Goody 1969, fig. 4), the Enchodontoidei and probably also the Halecoidei fall in the second (Goody 1969, figs. 42, 48, 64, 69), and information is lacking on the caudal skeleton of Cimolichthyoidei.

Such a division correlates rather well with the development of the neural spine of the second pre-ural centrum, which is long in all members of the first group, short in various representatives of all suborders except stomiatoids in the second. A further consequence of a division along these lines would be that the first group is related to

the ostariophysans, the second to the neoteleosts, each group containing a primitive basal suborder (alepocephaloids in the first, salmonoids in the second) and a series of more advanced groups foreshadowing or paralleling the major radiations of the ostariophysans and neoteleosts. In the ostariophysans and neoteleosts, however, correlation with the development of the neural spine of PU2 is not perfect, for although a short neural spine is characteristic of primitive neoteleosts, it is also found quite frequently in ostariophysans (*s.str.*), apparently as an individual variation (cf. Monod 1968, figs. 456–521). Should future investigations support such a division of the Euteleostei, it may be possible to do away with the Protacanthopterygii (or to reserve this name for the salmonoid-osmeroid group).

(c) Comparisons with *CLUPAVUS* and the CLUPAVIDAE

The genus *Clupavus* was erected by Arambourg (1950 : 417) for a group of uppermost Jurassic (Purbeckian) and Cretaceous species of *Leptolepis* similar to the Purbeckian *L. brodiei* Agassiz, selected as type-species. *Clupavus* was said to be intermediate between *Leptolepis* and the Dussumieriinae. In 1955 (p. 33) Arambourg placed *Clupavus* in the Clupeidae and listed ten species of the genus in addition to *C. brodiei* (but including *Leptolepis valdensis* Smith Woodward, previously transferred to *Anaethalion* by Smith Woodward (1919 : 126)). In the *Traité de Zoologie*, Bertin & Arambourg (1958 : 2230) erected the family Clupavidae, with *Clupavus* as the only contained genus, which they placed in the Clupeoidei, commenting further on its relationship to leptolepids and clupeoids.

Recently (1968) Arambourg has published a 'rectification de nomenclature' on *Clupavus*, stating that he now recognises *Leptolepis brodiei* as a true *Leptolepis*, and ("afin d'éviter toute discussion byzantine ultérieure") replacing it as type-species of *Clupavus* by *C. maroccanus* Arambourg (1968), a species based on material from the Lower Cenomanian of Morocco which was previously (1955) described as *Clupavus* cf. *neocomiensis* Bassani. I have examined the type material of *L. brodiei* and I agree with Arambourg that the fish shows nothing to distinguish it from *Leptolepis s.l.* Arambourg's emendation of the type-species of *Clupavus* will have to be ratified by the International Commission (Article 70 of the 'Code'), but I accept it here since it clarifies the meaning of *Clupavus*, and since *C. maroccanus* is almost the only species referred to the genus on which any sort of detailed anatomical information is available in the literature.

Clupavus maroccanus is a small fish which is superficially, and in many details of the skull, vertebral column and fins, so like *Gaudryella* and *Humbertia* that in 1967, before recognising the differences between the latter, I confidently assigned the Lebanon fishes to *Clupavus*. Through the kindness of Prof. C. Arambourg and Mlle J. Signeux I have been able to examine some of the type material of *C. maroccanus* from Jebel Tselfat, Morocco. This material is so preserved that it is not possible to elucidate many details of the skull, and no very detailed comparison with *Gaudryella* and *Humbertia* can be made. *C. maroccanus* resembles *Gaudryella* rather than *Humbertia* in the following characters :

1. Trunk relatively compressed, since the fish is frequently preserved in lateral view.

2. Ethmoid strongly ossified and of complex shape.
3. Branchiostegals rather numerous (about 10) and slender.
4. Premaxilla toothless.
5. Subopercular smaller than opercular.
6. Pelvics below 21st or 22nd vertebra.
7. Dorsal originating over 15th vertebra, with 12 rays.
8. Caudal scutes absent or very small.

This list contains a few advanced characters, while the features in which *C. maroccanus* resembles *Humbertia* rather than *Gaudryella* seem to be all primitive (parietal branch of supraorbital canal large ; head of hyomandibular single ; metapterygoid large). There is some evidence here that *Clupavus* is closer to *Gaudryella* than *Humbertia*, but in the apparent absence of teeth on any bone, *C. maroccanus* differs from both *Gaudryella* and *Humbertia*.

The most valuable evidence comes from the caudal skeleton. *C. maroccanus* has the first pre-ural and ural centra fused, like *Gaudryella* and *Humbertia*, and is therefore probably a euteleostean, not a clupeomorph (this is also indicated by the well developed articular head of the first hypural, which is absent or reduced in clupeomorphs). Several potentially important features of the caudal skeleton cannot be seen in *C. maroccanus* (presence or absence of a second ural centrum, a urodermal and a third uroneural, number of epurals, etc.), but there are three characters which distinguish it from *Gaudryella* and *Humbertia* : first, the first uroneural does not extend on to the second pre-ural centrum ; second, there is a complete neural spine on the second pre-ural centrum, and this is a constant feature of the species, just as the short neural spine is constant in *Gaudryella* and *Humbertia* ; third, there appears to be a short neural arch on PU1 + U1, which is separate from the first uroneural, much as in *Argentina* (npu1, Fig. 38). These last two characters would place *Clupavus* on the left hand side of the diagram in Fig. 47, suggesting that it may be related to the argentinoids, but can hardly be close to *Gaudryella* or *Humbertia*. For these reasons, neither *Gaudryella* nor *Humbertia* can be included in the Clupavidae.

Other species which have been referred to the Clupavidae by Arambourg and subsequent workers are listed below, with brief notes on their significance.

Leptolepis formosus Traquair, *L. attenuatus* Traquair, *L. brevis* Traquair. These three species are from the Wealden (continental lowermost Cretaceous) of Bernissart, Belgium (Traquair 1911). None has been redescribed since Traquair's work, and the holotypes of *L. formosus* and *L. attenuatus* are now lost. From the published descriptions one can learn nothing of value in deciding on their status, but from their age it is unlikely that they can have much to do with *Clupavus*, *Gaudryella* or *Humbertia*.

Leptolepis neocomiensis Bassani, *L. neumayri* Bassani, *L. checchiai* d'Erasmus, *L. aff. voithi* Agassiz. These four species are from Albo-Aptian (Pietraroia, Castellammare) and Cenomanian (Lesina, Comen and neighbouring localities) deposits in Italy and Jugoslavia.

L. neumayri (Bassani 1882 : 14), from the Lower Cenomanian of Lesina and Comen, was transferred to the myctophoid genus *Leptosomus* (= *Cassandra*, a

synonym of *Sardinioides* according to Goody 1969) by d'Erasmus (1964 : 103) and this is certainly correct.

L. neocomiensis, which has often been synonymised with *L. brodiei* Agassiz, is recorded at Pietrarroia (d'Erasmus 1915, as *L. brodiei*), Castellammare (Bassani & d'Erasmus 1912, as *L. brodiei*), Lesina (Bassani 1882) and Comen (d'Erasmus 1946). The species is superficially similar to *Clupavus maroccanus*, for Arambourg at first described the latter as *C. cf. neocomiensis*. Between the four populations of *L. neocomiensis* cited above (that from Castellammare described on only two specimens), there is considerable variation in meristic characters (proportions, fin-ray and vertebral counts), and apart from these features there is very little in the descriptions on which comparisons can be based. The BM(NH) contains one specimen from Castellammare (P.3612), cited by Bassani & d'Erasmus (1912 : 230), which agrees well enough with their description of *L. brodiei*. This specimen is poorly preserved and yields no detailed information in the skull. But there are epipleurals in the middle part of the trunk, suggesting that it is not a *Leptolepis* (which has epineurals only), while the neural spine of PU₂ is short and there are large caudal scutes, distinguishing it from *Clupavus*. These two characters of the tail are primitive features also present in *Humbertia*, but there is no information regarding most of the characters in which *Humbertia* differs from *Gaudryella* and no means of telling whether it resembles one of these genera more than the other.

The BM(NH) also contains two specimens from Comen (P.10617-8) which agree with the population of *L. neocomiensis* described from there by d'Erasmus (1946). These fishes are fairly well preserved, though bituminised, and the caudal skeleton (Fig. 48) shows a short neural spine on PU₂, a stegural of normal form, three epurals, PU₁ and U₁ fused, and the characteristic salmoniform expansions on the last few neural and haemal spines. The last two characters show that it is a euteleostean fish, and the neural spine of PU₂ and the stegural distinguish it from *Clupavus*. This caudal skeleton is rather like those of *Gaudryella* and *Humbertia*, though the preservation is not good enough for detailed comparisons, but the fish is easily distinguished from them by the smaller vertebral number and more numerous caudal vertebrae (34 vertebrae, 16-17 caudals ; d'Erasmus gives 32-36, c. 18 caudal), by having only 9 pelvic rays, and by the deeper trunk (depth about 25% standard length). In the skull, the lower limb of the preopercular is much shorter than in *Gaudryella* and *Humbertia*, there is a robust, toothless premaxilla, a long, slightly curved maxilla which extends back to the quadrate and bears rather large teeth, a heavily ornamented posterior supramaxilla, and a short series of rather large teeth on the lower jaw.

L. aff. voithi Agassiz, described from Castellammare by Bassani & d'Erasmus (1912 : 231) on the basis of five specimens, is similar to *Clupavus*, *Gaudryella* and *Humbertia* in proportions, fin positions and vertebral number (40 vertebrae, 15 caudal), but has a larger dorsal fin (16 rays). From the published description there is no evidence to suggest that it is closer to one of these genera than to the others.

L. checchiai d'Erasmus (1946 : 37), described on the basis of ten specimens from Comen, appears to have PU₁ and U₁ fused and has a large subopercular and 36-38 vertebrae, resembling *Humbertia* rather than *Clupavus* or *Gaudryella*, but there is a

complete neural spine on PU2 (d'Erasmus 1946, fig. 13C) and the anal fin lies well forward, closer to the pelvics than to the caudal. Once again, there is no means of deciding on the relationships of this species.

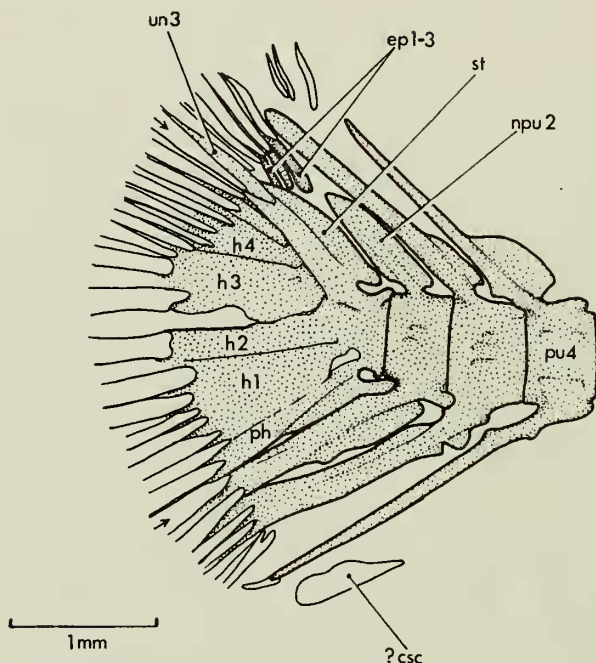


FIG. 48. '*Leptolepis*' *neocomiensis* Bassani, Lower Cenomanian, Comen, Yugoslavia. Caudal skeleton as preserved in P.10617. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

Leptolepis congolensis Arambourg & Schneegans (1936 : 13) is from the Cocobeach series of Angola. These continental beds have recently been placed in the Wealden on the evidence of ostracods (Grekoff & Krömmelbein 1967). *L. congolensis* is superficially similar to *Clupavus*, *Gaudryella* and *Humbertia*, but has a deeper trunk (c. 25% of the standard length) and the pelvics are inserted below the origin of the dorsal. The subopercular is large, teeth are few or absent and no epipleurals have been seen. Arambourg & Schneegans' drawing of the caudal skeleton (1936, fig. 8) is schematic, but it shows PU1 and U1 fused, a short neural spine on PU2, and large caudal scutes. The last two characters distinguish it from *Clupavus* and the large caudal scutes suggest that it is not close to *Gaudryella*. Further information is necessary before anything positive can be said about its relationships.

Clupavus yamangiensis Casier and *C. longicaudatus* Casier are from early Cretaceous deposits in the Congo (Casier 1961 : 54, 57). Each is based on a single defective specimen and very little is known of them. *C. yamangiensis* is described as having no teeth, no large coronoid process on the dentary, a very short dorsal fin and

the pelvic and anal fins further forwards than they are in *Clupavus*, *Gaudryella* and *Humbertia*. In the caudal skeleton (N. Bonde, personal communication) PU1 and U1 appear to be fused and there is a full neural spine on PU2 and a shorter neural spine on PU1, the last two characters suggesting relationship with *Clupavus*. There are only eighteen principal caudal rays, which would distinguish the species from all others under consideration here.

C. longicaudatus is said by Casier to have 25 or less vertebrae, many fewer than any other supposed clupavid. But the single specimen is badly distorted and no diagnostic characters are preserved (N. Bonde, personal communication).

Paraclupavus caheni Saint-Seine & Casier (1962 : 30) is from the Kimmeridgian (Upper Jurassic) of Songa, Congo. It is a primitive form, with three supraorbitals, a large basipterygoid process, long parietals, very large post-temporals, and 17-18 branchiostegal rays. Although three series of intermuscular bones are mentioned in the original description, N. Bonde (personal communication) finds that there are epineurals only, as in leptolepids, that PU1 and U1 are separate, and that each bears a small neural arch. *Paraclupavus* appears to be a relative of the leptolepids, from which it differs principally in the reduced number of vertebrae (34), the absence of pit-lines or a branch of the supraorbital canal on the parietal, the slender infra-orbitals, and the absence of scales.

Leptolepis nevadensis David (1941) is referred to *Clupavus* by Lehman (1966 : 191). This species is based on about a dozen specimens from the Lower Cretaceous Weber Conglomerates of Nevada. It has 49-50 vertebrae (15 caudal), more than any other 'clupavid', and has epineurals only. No teeth have been seen. In the caudal skeleton (David 1941, fig. 3 ; personal observations) the neural spine of PU2 is complete and there are small neural arches on PU1 and U1 which are distinct from the first uroneural, PU1 and U1 are separate and there are large caudal scutes. Separation of PU1 and U1 distinguish the species from *Clupavus*, *Gaudryella* and *Humbertia* and place it in some more primitive group, but nothing positive can be said about its relationships.

Clupavus casieri Taverne (1969) is based on numerous specimens from the Upper Santonian of Vonso, Congo. The species is said by Taverne to be very similar to *C. maroccanus*. Like the latter it is toothless, but it has only 35-37 vertebrae (less than in *C. maroccanus* or *Gaudryella*) and a rather long anal fin, with fifteen rays, many more than in *C. maroccanus*, *Gaudryella* or *Humbertia*. There appears to be a complete neural spine on PU2, a difference from *Gaudryella* and *Humbertia* and a resemblance to *Clupavus*. Almost nothing is known of the skull or caudal skeleton, and nothing can yet be said on its relationships.

Bonde (1966 : 199) has referred to the Clupavidae an undescribed fish which is common in the Lower Eocene Mo-clay of Denmark. He now believes (personal communication) that this fish cannot be positively referred to the Clupavidae but that it is a primitive salmoniform whose relationships remain to be discovered.

From this survey it is clear that the family Clupavidae, as now constituted, is not a useful taxon. Although all the fishes placed in the family are superficially similar, they are easily distinguished from *Clupavus maroccanus*, the only undoubted clupavid, wherever detailed information is available. Supposed clupavids seem to fall into

three categories. First, and most numerous, are those species which are so poorly preserved or described that nothing is known which might bear on their relationships : *Leptolepis formosus*, *L. attenuatus*, *L. brevis*, *L. neocomiensis* (the population from Comen excepted), *L. aff. voithi*, *Clupavus longicaudatus*, *C. casieri*. Second, there are two species, *Paraclupavus caheni* and *Leptolepis nevadensis*, which have the first pre-ural and ural centra separate and therefore belong to some more primitive group than that containing *C. maroccanus*. Third, there are four species, *Leptolepis neocomiensis* (population from Comen), *L. checchiai*, *L. congolensis* and *Clupavus yamangiensis*, which have the first pre-ural and ural centra fused, like *Clupavus*, *Gaudryella* and *Humbertia*. These four species then fall into two groups, those with a short neural spine on PU₂, *L. neocomiensis* and *L. congolensis*, and those with a long neural spine on PU₂, *L. checchiai* and *C. yamangiensis* ; only the last two species are probable members of the Clupavidae. All that can be said of the Clupavidae at present is that they appear to be euteleostean fishes, not clupeomorphs, and that the structure of the caudal skeleton in the type-species suggests a possible relationship to the argentinoids. *Leptolepis neocomiensis* and *L. congolensis* are possible relatives of *Gaudryella*, *Humbertia* or the osmeroids and stomiatoids, but the available information does not allow a decision. *L. congolensis*, because of its Wealden age, may prove to be of particular interest.

(d) Comparison with other Cretaceous teleosts

Bassani (1882 : 31) and Kramberger (1895 : 37) have referred to *Clupea gaudryi* (= *Gaudryella gaudryi*) specimens from the Lower Cenomanian of Lesina, Comen and Mrzlec (near Solkan, Jugoslavia). Bassani's two specimens from Lesina agree with *Gaudryella* rather than *Humbertia* in the position of the dorsal fin (origin over the seventeenth vertebra ; predorsal length c. 45% standard length), the apparently toothless premaxilla (Bassani 1882, pl. 7, fig. 2), small subopercular, and in having 42 vertebrae (but there are said to be 18 caudal vertebrae and only 18 pairs of ribs, while *G. gaudryi* has only 15 caudals and about 26 pairs of ribs). In having 14 dorsal rays the specimens resemble *Humbertia* rather than *Gaudryella*. These fishes differ from both *Gaudryella* and *Humbertia* in having a larger anal fin (11 rays), apparently no epipleurals, and, according to Bassani, traces of abdominal scutes. This last character may well be an error, for similar traces were described in the material of *G. gaudryi* by Pictet & Humbert. It is possible that Bassani's specimens are close to *G. gaudryi*, but most of the characters which distinguish *Gaudryella* and *Humbertia* are not determinable in them, and nothing is known of the caudal skeleton.

Kramberger (1895 : 37, pl. 8, figs. 3, 4) referred two specimens to *C. gaudryi*, one from Mrzlec (fig. 3) and one from Comen (fig. 4). According to d'Erasmus (1946 : 37) the second of these is *Leptolepis neocomiensis*, the first *Scombroclupea gaudryi*, which in d'Erasmus's usage is a clupeomorph fish. Kramberger did not describe the specimens but only gave a series of measurements and counts taken from the Mrzlec individual. This has a rather large, toothed premaxilla and 38 vertebrae (14 caudal), as in *Humbertia*, but the subopercular is small, the dorsal is set further back than in either *Humbertia* or *Gaudryella* and has only ten rays, while the lower jaw appears to be more slender than it is in *Humbertia* and *Gaudryella*. Once again, nothing is

known of the majority of the features in which *Gaudryella* and *Humbertia* differ, and nothing is known of the caudal skeleton.

Apart from the various European and African Cretaceous *Leptolepis* species referred to *Clupavus* which have been discussed in the previous section, there are several American *Leptolepis*-like species which might be related to *Gaudryella* or *Humbertia*. As in the clupavids, most of these are very poorly known and where nothing can be deduced about their relationships they will merely be listed.

Leptolepis bahiaensis Schaeffer (1947 : 13) and *Scombroclupeoides scutata* Smith Woodward (1908 : 360). These species are from the Neocomian (non-marine lower-most Cretaceous) of Bahia, Brazil. Schaeffer (1947, table 1) placed them in the Upper Cretaceous, but recent work on ostracods (Krömmelbein 1962, Grekoff & Krömmelbein 1967) has shown that the beds correlate with the European and West African Wealden. *Scombroclupeoides scutata* was described by Smith Woodward as a clupeoid, since he found traces of abdominal scutes and thickened scales behind the anal which he compared to the scutes associated with the anal finlets in *Scombroclupea*. But the type material of the species (P.10570-1) shows that the so-called abdominal scute is the front part of the left opercular and subopercular, and the post-anal scutes appear to be lateral line scales. There is thus no evidence that this fish is a clupeoid, but positive evidence of its relationships is lacking since the caudal skeleton is not preserved and the skull is very deficient. Epipleurals are present, suggesting that it is not a *Leptolepis*, but otherwise it is very like Schaeffer's *L. bahiaensis*. The latter is described as having no epipleurals and no caudal scutes, while there is a large caudal scute in *S. scutata*. The Bahia series is correlated with the Cocobeach series of West Africa, and one or both of these Brazilian species could well be close to or synonymous with *Leptolepis congolensis* (p. 286).

Leptolepis tamanensis Dunkle & Maldonado-Koerdell (1953) is from Neocomian beds in Mexico. The only specimen has a *Gaudryella*-like ethmoid region, but is very incomplete.

Leptolepis diasii Santos (1958) is from the Santana Formation of Ceara, Brazil. These marine or estuarine beds were formerly considered to be Upper Cretaceous, but recent workers place them in the Lower Albian or Upper Aptian (Santos & Valença 1968, Beurlen 1970). The fish has 33-34 vertebrae with ten caudal, many fewer than *Gaudryella* and *Humbertia*.

Leptolepis australis de Saez (1939), *L. leanzai* de Saez (1949), *Tharrhias feruglioi* Bordas (1943) and *T. shamani* de Saez (1949) are all from the continental Upper Cretaceous of Chubut, Argentina. Nothing useful is known of them.

One last Cretaceous fish that must be mentioned is *Idrissia jubae* Arambourg (1955 : 77), from the Lower Cenomanian of Jebel Tselfat, Morocco. Arambourg described this as a primitive member of the Stomiatoidei and placed it in the family Gonostomatidae. Weitzman (1967b: 536) discussed *Idrissia* in his review of fossil stomiatooids and pointed out that there was no reason to regard it as a gonostomatid or even as a stomiatooid relative, principally because of lack of information on its structure. *I. jubae* is superficially very like *Gaudryella* and *Humbertia*, with 40 vertebrae (14 caudals), epineurals and epipleurals on the abdominal vertebrae, a vertical hyomandibular and a small mouth. It differs from *Gaudryella* and *Hum-*

bertia in having a slightly deeper trunk and longer head, the dorsal fin set further back (origin over nineteenth vertebra), a longer anal fin (13 rays), short, slender ribs, and a rather shallow mandible. The premaxilla is toothed and the subopercular is large, as in *Humbertia*, but there are about ten branchiostegals and the pelvics are inserted below the twenty-first vertebra, as in *Gaudryella*.

Apart from the species mentioned in this section and the preceding one, all other Cretaceous teleosts seem to differ markedly from *Gaudryella* and *Humbertia*, and the majority belong to easily recognised groups. One must conclude that although there are various species which resemble *Gaudryella* and *Humbertia*, all are too poorly known for any detailed comparisons and many of these resemblances are simply characters of relatively generalised teleosts. There is no fossil species which can be shown to be more like one of these genera than the other, and therefore no evidence that they are not each other's closest relatives.

V. SUMMARY

1. Two small, superficially *Clupavus*-like or *Argentina*-like fishes are described as *Gaudryella* gen. nov. *gaudryi* (Pictet & Humbert) and *Humbertia operta* gen. & sp. nov. These two monotypic genera are known only in the Middle Cenomanian fish beds of Hakel and Hajula, Lebanon. *Gaudryella gaudryi* is the commonest fish at Hajula but is uncommon at Hakel ; it outnumbers *Humbertia operta* by about three to one at both localities.

2. Because of abundant material which is amenable to acid preparation, the structure of these two species can be worked out in some detail. This excess of knowledge severely limits comparisons with other superficially similar Cretaceous species, none of which is known in comparable detail, and useful comparisons can only be made with living fishes.

3. *G. gaudryi* and *H. operta* share many osteological features (p. 250), apart from overall similarities in body form and fin disposition. The majority of these shared features are primitive teleostean characters, but fusion of the first pre-ural and ural centra, the development of a stegural, passage of the supratemporal commissure in a groove across the parietals, an almost entirely acellular skeleton, and a few other advanced features show that both genera are members of the Euteleostei.

4. There are many differences between *Gaudryella* and *Humbertia* (Table 3), the most striking of which include the form of the ethmoid ossifications (very primitive in *Gaudryella*, *Argentina*-like in *Humbertia*), the distribution of the dentition, the shape and number of the branchiostegals, the presence of a small basipterygoid process and a sutured ceratohyal in *Humbertia*, and fusion between the two posterior infraorbitals, between the pelvic splint and girdle, and within the caudal skeleton in *Gaudryella*. Despite these differences, it is not possible to show that either genus is more closely related to any living or contemporary fish than is the other, or that statements about the relationships of one are not equally true of the other.

5. Amongst euteleostean fishes, there is no evidence in *Gaudryella* or *Humbertia* of the specialisations which characterise the Ostariophysi or the Neoteleostei, and the two genera are placed in the Salmoniformes. Although *Gaudryella* and *Humbertia* resemble the argentinoids in many ways, any close relationship is improbable because

of the cellular skeleton and lack of a stegural in the latter. The only salmoniform groups with which they show positive evidence of relationship are the osmeroids and stomiatoids, especially the hypomesine osmerids, but they are much more primitive than any known member of these suborders and are placed as *Salmoniformes incertae sedis*.

6. The ossifications of the ethmoid region in teleosts are reviewed and it is concluded that a single, peri- and endochondrally ossified mesethmoid and a separate dermal rostral are primitive for teleosts. Paired proethmoids are certainly homologues of the median rostral, but it is not possible to decide which arrangement is the more primitive. The numerous ethmoid ossifications of osmerids and stomiatoids are an advanced feature relating the two groups.

7. The jaws and palate of *Gaudryella* and *Humbertia* are more like those of *Hypomesus* than any other osmeroid or stomiatoid. Evidence is presented that *Hypomesus* is the most primitive osmerid, and that these resemblances may therefore be significant. The large mouths and long, shallow lower jaw of osmerines and the larger mouths of stomiatoids may be successive modifications from a *Hypomesus*-like proto-osmerid.

8. The structure of the caudal skeleton in euteleosteans is reviewed and it is found that they fall into two groups according to whether the neural arch of PU1 (and UI where this exists) fuses with the underlying centrum, or with the first uroneural to produce a stegural (Fig. 47). The first of these groups, without a stegural, contains the alepocephaloids, argentinoids, galaxioids and ostariophysans; the second, with a stegural, the salmonoids, esocoids, *Gaudryella* and *Humbertia*, osmeroids, stomiatoids and neoteleosts. The development of the neural spine of PU2 correlates with such a division. The structure of the caudal skeleton indicates that the Prototroctidae and Retropinnidae are osmeroids, not galaxioids.

9. In general, the caudal skeleton seems to be a more reliable guide to relationships (at the level under discussion in this paper) than any known feature or combination of features in the skull, vertebral column or fins. This may well be only because the caudal skeleton is relatively simple and easy to interpret in comparison with the skull, where the significance and the interaction of many features are still poorly understood. But the reliability of the caudal skeleton can be of great value to palaeontologists, for the details of the tail can often be made out in otherwise unpromising fossils.

10. Species placed in the late Jurassic and Cretaceous family Clupavidae are reviewed, and it is concluded that they show no evidence of close relationship. Most of these species are so poorly known that nothing can be said about their relationships. The type-species of *Clupavus*, *C. maroccanus*, is apparently a euteleostean, not a clupeomorph, but it is not close to *Gaudryella* and *Humbertia*.

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VII. ABBREVIATIONS USED IN FIGURES

acv	foramen of anterior cerebral vein	npuz	neural spine of second pre-ural centrum
Ao	antorbital	nu1	neural arch of first ural centrum
arpm	articular process of premaxilla	Op	opercular
Art	angulo-articular	Ors	orbitosphenoid
Asp	autosphenotic	Pa	parietal
aspm	ascending process of premaxilla	Pal	palatine
Bh	basihyal	Pas	parasphenoid
Bht	basihyal tooth plate	Pch	proximal ceratohyal
Boc	basioccipital	pfmx	palatine condyle on maxilla
bpt	basipterygoid process	ph	parhypural
Brr	branchiostegal ray	Pmx	premaxilla
Cl	cleithrum	Pop	preopercular
Cor	coracoid	Pro	prootic
csc	caudal scute	ptf	opening of post-temporal fossa
Dch	distal ceratohyal	ptfc	posterior opening of trigemino-facialis chamber
Den	dentary	Pto	pteric
Dsp	dermosphenotic	Pts	pterosphenoid
Ecp	ectopterygoid	Ptt	post-temporal
Enp	endopterygoid	pu1 + u1	compound centrum containing first pre-ural and ural centra
ep	epural	pu3-4	third and fourth pre-ural centra
Epo	epiotic	Qu	quadrate
epsa	foramen or groove for efferent pseudobranchial artery	Ro	rostral
Exo	exoccipital	Rrt	retroarticular
fh	hypural foramen (between first and second hypurals)	Sca	scapula
fhm	articular surface for hyomandibular	Scl	supracleithrum
fica	foramen of internal carotid artery	scr	ossified sclerotic
fofn	foramen of otic branch of facial nerve	Sma	anterior supramaxilla
fph	parhypural foramen (between parhypural and first hypural)	Smp	posterior supramaxilla
Fr	frontal	So	supraorbital
h1-6	hypurals	Soc	supraoccipital
hap	hypurapophysis	son	foramina of superficial ophthalmic nerves
Hhl	lower hypohyal	Sop	subopercular
Hhu	upper hypohyal	st	stegural
Hm	hyomandibular	Stt	supratemporal
hmx	cranial condyle of maxilla	stv	foramen of supratemporal branch of vagus nerve
Ic	intercalar	Sym	symplectic
Io2-5	infraorbitals	u2	second ural centrum
Iop	interopercular	ud	urodermal
Lac	lachrymal	Uh	urohyal
Le	lateral ethmoid	un1-3	uroneurals
Mes	mesethmoid	Vo	vomer
Mpt	metapterygoid	IV, VIIhm,	foramina of trochlear, hyomandibular trunk of facial, glosso-pharyngeal and vagus nerves
Mx	maxilla	IX, X	
myo	posterior opening of myodome		
Na	nasal		
npur	neural arch of first pre-ural centrum		